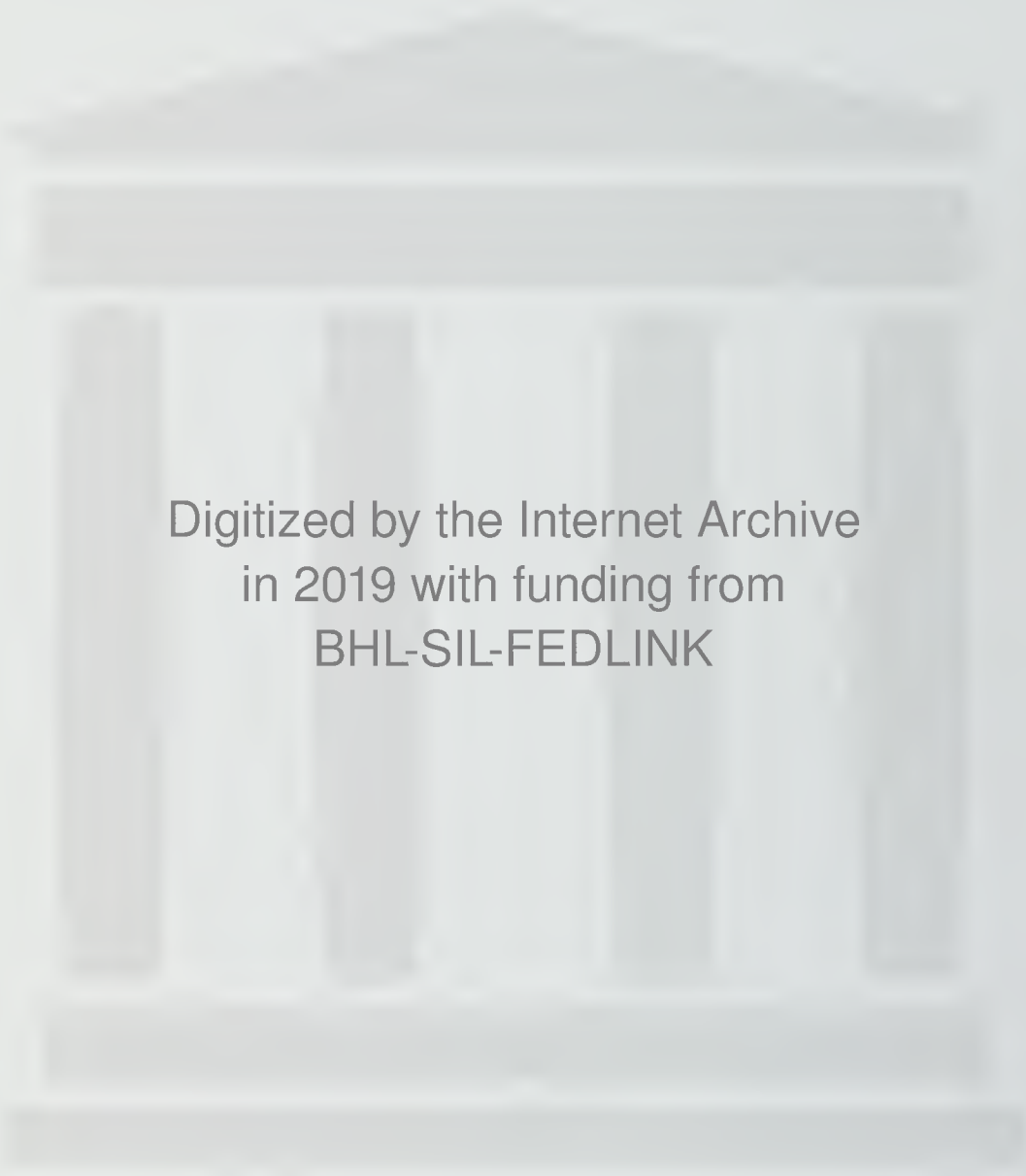


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**Note: In addition to this volume, 10 folded maps are
included with this issue.**

Biota of the Virginia Barrier Islands: Symposium Introduction

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The Virginia barrier islands extend 150 km along the seaward margin of the Delmarva Peninsula, from Assateague Island in the north to Fishermans Island in the mouth of Chesapeake Bay. This area includes 14 barrier islands and intervening inlets, numerous marsh islands, and extensive shallow bays, tidal flats and salt marshes. This coastline developed during the late Holocene rise in sea level (Shideler *et al.*, 1984). The time of formation of the islands and marshes was similar to that of other barrier islands along the mid-Atlantic coast, about 5,000 to 6,000 BP (Newman and Munsart 1968). The biological communities which occupy the modern islands are the product of less than 5,000 years of development. Given their susceptibility to recurrent disruption by storms and flooding, most of these communities have existed for much less than 5,000 years.

This barrier-lagoon complex has undergone continuous, rapid change as sea level has risen. The islands have migrated landward by means of erosion on their seaward margin and sand movement across the islands to the lagoons by overwash and inlet formation (Dolan *et al.*, 1979). The modern islands continue to experience shoreline recession, with local rates as high as 13 m per year (R. Dolan, pers. comm.). Migration has the effect of continually eroding, burying, raising and rearranging the elements of the barrier island landscape. In effect, there is an on-going, perpetual experiment in ecosystem disturbance, biotic responses and community development. The islands thus comprise an ideal natural laboratory for studies of ecology and evolution.

Although the islands have been inhabited sporadically since the arrival of Captain John Smith in 1608 (Graham 1976), most remain isolated, uninhabited and relatively natural (Dueser *et al.* 1976). The Nature Conservancy in 1970 designated 14,170 ha of islands and marshes as the Virginia Coast Reserve, dedicated to conservation, education and research (Cutler and Jenkins 1976). Most of the marsh and island acreage outside the Reserve is under federal or state control, including Assateague Islands National Seashore; Chincoteague, Eastern Shore of Virginia, and Fishermans Island National Wildlife Refuges; and Wreck Island Natural Area.

This dynamic system has attracted the attention of many researchers during the past 20 years. A symposium entitled "The Biota of the Virginia Barrier Islands" was convened in May 1988, to bring together biologists working on diverse aspects of the island biota. The 16 papers included here represent a diverse array of taxa, habitats and topics, and are a direct result of the discussions which followed the

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symposium. These papers represent the most comprehensive introduction available to the biota of the Virginia barrier islands. It is hoped this volume will prove useful to future researchers and to those charged with the stewardship and management of these islands.

ACKNOWLEDGEMENTS

Many individuals played vital roles in bringing this project to completion. John M. Hall and Barry Truitt of the Virginia Coast Reserve encouraged much of the research reported here. Richard S. Sojka and Donald R. Young chaired sessions during the symposium. Joseph C. Mitchell generously assisted with the final editing of the manuscripts. James H. Martin, editor of the Virginia Journal of Science, encouraged publication of this symposium volume and made numerous concessions to accommodate inclusion of over-size tables and figures. The authors patiently awaited publication as the volume slowly came together. Their patience far surpassed what would normally be expected. Preparation and publication of this volume was assisted by the Virginia Coast Reserve Long-Term Ecological Research Program of the University of Virginia (NSF BSR-8702333).

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Preliminary Vascular Flora for the Virginia Barrier Islands

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ABSTRACT

Vegetation on 16 barrier and marsh islands located along the southern Delmarva Peninsula was studied in 1975. From north to south, the islands included Metompkin, Cedar, Parramore, Revel, Crescent, Chimney Pole Marsh, Hog, Rogue, Cobb, Little Cobb, Wreck, Ship Shoal, Godwin, Myrtle, Mink, and Smith Islands. Variations in dominant island characteristics included thickets and pine-hardwood forests; xeric to mesic grasslands; salt marsh; and bare, overwashed sand. Representatives of 67 vascular plant families, 151 genera and 217 species or varieties were collected. These included two northern limits, one southern coastal limit, three coastal outliers, and six northern outliers. Several species common on the mainland were uncommon or found on few islands. Five oak species (*Quercus* spp.) occurred only on Smith Island. Red maple (*Acer rubrum*) was found only on Parramore and Smith Islands. Ferns were observed on Parramore, Cobb and Smith Islands. Six planted and 23 naturalized species were observed. The effects of island dynamics, human activities, and plant dispersal mechanisms are evident in the island flora.

Key Words: barrier island, Delmarva Peninsula, plant species, vascular flora

INTRODUCTION

Preliminary plant species lists were compiled in the process of preparing vegetation maps and accompanying community descriptions for 16 of the barrier and marsh islands which lie along the seaward margin of the Delmarva Peninsula (McCaffrey 1975, 1976). Comprehensive species lists and vegetation descriptions have been published for Assateague Island (Higgins *et al.* 1971, Hill 1986), Wallops Island (Klotz 1986), and Fishermans Island (Boulé 1979). Less intensive surveys have been reported for Parramore Island (Harvill 1965) and Smith Island (Clovis 1968). These studies reveal substantial inter-island variation in plant diversity, species composition, and vegetation structure. This study was designed to extend the scope of the previous studies of Parramore and Smith Islands, and to provide an initial inventory of plant species on 14 additional islands. Issues of particular interest included the frequency of unique species occurrences, the distributions of tree, shrub and fern species, the distributions of species at or near the limits of

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their geographic ranges, and the distributions of planted and naturalized species. McCaffrey and Dueser (1990) present vegetation maps and community descriptions for these 16 islands.

STUDY AREA

The study islands extend 75 km north to south along the seaward margin of Accomack and Northampton Counties, Virginia, and are centered approximately on latitude 37° 30' N and longitude 75° 40' W. They include Metompkin, Cedar, Parramore, Revel, Crescent, Chimney Pole Marsh, Hog, Rogue, Cobb, Little Cobb, Wreck, Ship Shoal, Godwin, Myrtle, Mink and Smith Islands (Fig. 1). Crescent Island is an accreting land mass which developed since around 1970 in the lee of the south end of Parramore Island. Most of the acreage on the study islands is owned by The Nature Conservancy, and managed as the Virginia Coast Reserve. Wreck Island is owned by the Commonwealth of Virginia. There are privately-owned tracts on Metompkin, Cedar, Hog and Smith Islands.

The islands lack modern human development, yet all have a history of human influence (Graham 1976). After the mid-1800's, several of the larger islands (Metompkin, Cedar, Parramore, Hog, Cobb, and Smith) supported hotels, sports clubs, summer cottages, and life-saving and Coast Guard stations. Revel Island had a hunting club. The town of Broadwater, Virginia, population 250 at the turn of the century, was located on the southern end of Hog Island until 1935. Probably all of the upland islands have been grazed by sheep, goats and cattle during the past century. All areas of Parramore, Rogue and Smith Islands have burned in the past. Cobb and Wreck Islands were burned regularly prior to the 1930's (Graham 1976). All of the islands are subjected periodically to high winds, flooding and storm overwash resulting from hurricanes and northeasters (Dolan *et al.* 1988). A hurricane in 1933 effectively ended all attempts at permanent human habitation on the islands. The most recent major storm prior to this study was the Ash Wednesday northeaster of March 7, 1962.

METHODS

Field work was performed in 43 days between late March and late July, 1975. In addition, brief reconnaissance visits were made in January and early October, 1975. From one to five days were spent on each island. Preliminary vegetation maps were prepared from low-altitude (1:20000) infrared aerial photography. These maps were ground-truthed, and plant community types identified, from field observations made along multiple transects positioned and oriented to cross all mapping units (≤ 23 total units). Species lists were compiled during this field work. Plant taxa which appeared to be frequent associates in each community type, or which were particularly conspicuous, were emphasized; less apparent taxa were not recorded systematically.

Nomenclature follows Radford *et al.* (1968) except for *Bassia hirsuta*, *Juncus gerardii*, *Persea palustris*, *Prunus maritima* and *Puccinellia fasciculata* which follow Fernald (1950). Specimens were identified by the late Harry E. Ahles of the University of Massachusetts or Dr. Wilbur H. Duncan of the University of Georgia. Voucher specimens were deposited with the office of the Virginia Coast Reserve in Nassawadox, Virginia, and with the herbarium of the University of Massachusetts.

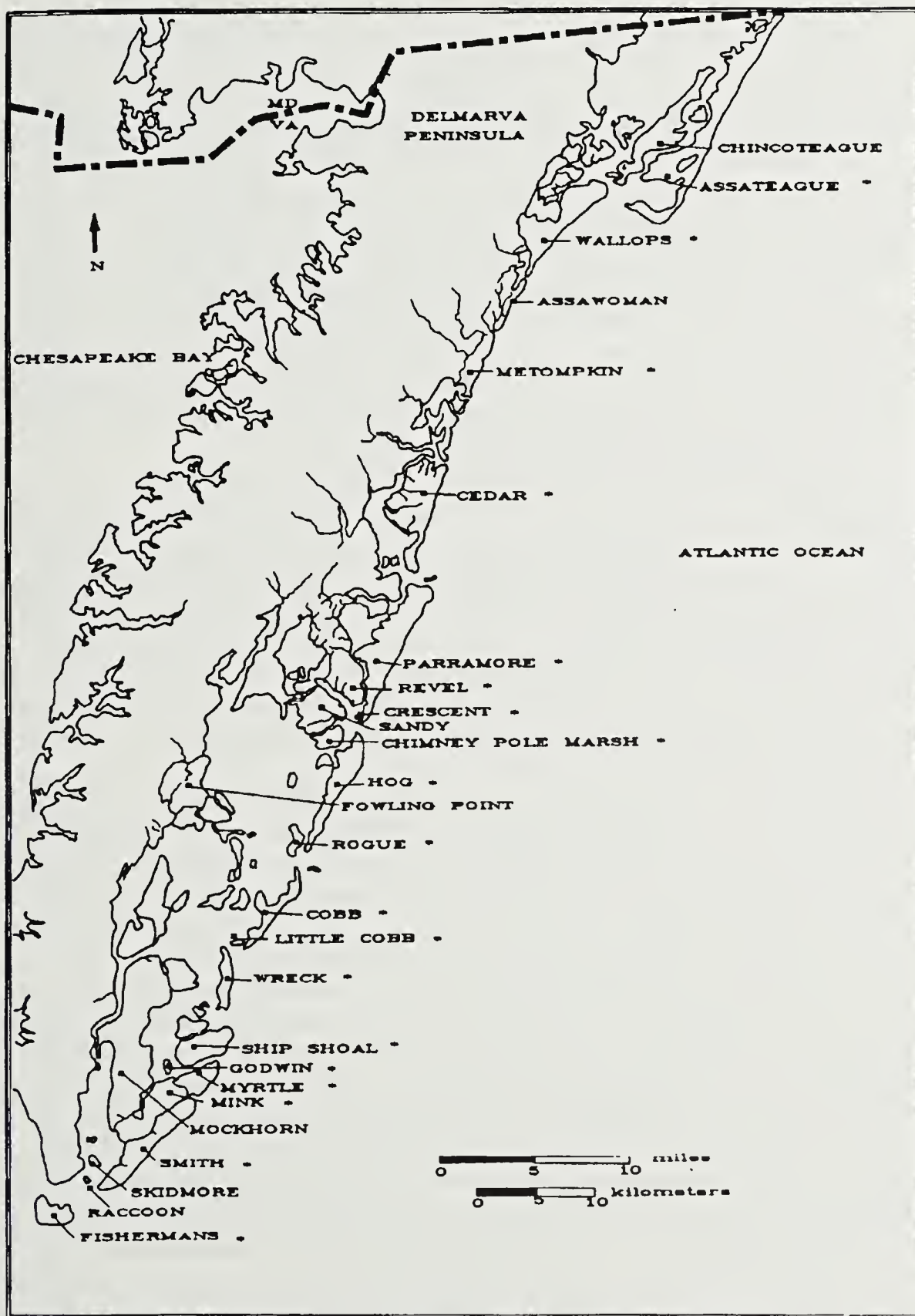


FIGURE 1. The Virginia Barrier islands extend the length of the seaward margin of the southern Delmarva Peninsula. Barrier and marsh islands referred to in this report are marked with an *.

RESULTS

Vegetation structure and complexity varied among islands (Table 1). The broader and more protected islands supported pine-hardwood forest (Parramore, Revel and Smith Islands) or tall (> 3 m) *Myrica cerifera* shrub thickets (Hog Island). These islands also had brackish marshes, and all but Revel Island had fresh marshes. The especially narrow, low-lying islands and those having a history of repeated fire (Rogue, Cobb, Wreck, Ship Shoal and Myrtle Islands; Graham 1976) supported dense *Spartina patens* grasslands or foredune-grasslands of *Ammophila breviligulata*. Metompkin, Cedar, Crescent, southern Hog, Little Cobb and northern Smith Islands were narrow and sparsely vegetated, and each exhibited evidence of past inlet opening and closure as well as overwash through broken dunes. The bayshore of each island consisted of *S. alterniflora* salt marsh. Chimney Pole Marsh and Mink Island were primarily marsh islands. Godwin Island was all salt marsh. McCaffrey and Dueser (1990) present detailed community descriptions and a 1:2000 vegetation map for each island.

A total of 217 taxa of vascular plants was recorded, including representatives of 67 families, 151 genera, and 217 species or varieties (Appendix 1). *Spartina alterniflora* occurred on all 16 islands, and was the only species observed on Godwin Island. Four species consistently occurred on all of the other 15 islands: *Solidago sempervirens*, *Cakile edentula*, *A. breviligulata*, and *Panicum amarum*. Two additional species, *Spartina patens* and *Salicornia virginica*, were missing only from Godwin and Little Cobb Islands. At the other extreme, 78 species (36%) were recorded on only one of the islands. The number of such unique species was one on Cedar Island and Chimney Pole Marsh, four on Metompkin, seven on Cobb, nine on Hog, 22 on Parramore, and 34 on Smith Island.

A total of 24 tree species were observed on 11 islands. *Juniperus virginiana* occurred on nine islands, *Pinus taeda* and *Prunus serotina* on six, and each of the 21 others on five or fewer islands. One tree species was found only on Cedar Island (*Maclura pomifera*), and one only on Parramore Island (*Celtis laevigata*). Fourteen species were found only on Smith Island (*Aralia spinosa*, *Paulownia tomentosa*, *Diospyros virginiana*, *Robinia pseudo-acacia*, *Quercus falcata*, *Q. laurifolia*, *Q. nigra*, *Q. stellata*, *Q. virginiana*, *Nyssa sylvatica*, *Amelanchier obovalis*, *Crataegus viridis*, *Sorbus arbutifolia* and *Ulmus americana*). Several species abundant in mainland forests were only minor components of forest on Parramore, Revel and Smith Islands. *Acer rubrum* on northern Parramore Island was represented by two small groups of trees totaling fewer than 25 individuals occurring on interior dunes near a fresh marsh. One tree had a 59 cm diameter at breast height. There was a group of 12 *A. rubrum* on a northern ridge on Smith Island. *Liquidambar styraciflua* was observed infrequently in pine and pine-hardwood forest on Parramore Island (7 individuals counted) and occasionally on Smith Island. *Robinia pseudo-acacia* and *Nyssa sylvatica* occurred only on Smith Island. *Quercus* was absent on all but Smith Island which had occasional *Q. falcata*, *Q. laurifolia*, *Q. nigra*, *Q. stellata*, and a few individuals of *Q. virginiana*. Except for a rare occurrence on Revel Island, *Ilex vomitoria* was found only on Smith Island where it was common. Several *I. vomitoria* saplings on Revel Island were in a line under a branch, suggesting avian seed dispersal as the source of this northern limit.

TABLE 1. Dominant physical and botanical attributes of 16 barrier and marsh islands for which preliminary flora are reported.

| Island | Features |
|--------------|---|
| Metompkin | Foredune-sparse grassland; dissected; overwash-and inlet-influenced |
| Cedar | North: juniper thicket with poison ivy South: sparse grassland; overwash-influenced |
| Parramore | Pine and hardwood forest; interior fresh marshes; brackish marshes; interior open dune-shrub thickets |
| Revel | Pine-hardwood forest |
| Crescent | Foredune-grassland; overwash-influenced |
| Chimney Pole | Marsh island with salt pond and grassland |
| Hog | North: accreting beach, salt flats; tall shrub thickets, dune-grassland, open dune-shrub thickets South: foredune grassland; erosion- and overwash- influenced |
| Rogue | Salt marsh with salt pond and dense grassland |
| Cobb | Dense <i>Spartina patens</i> grassland with xeric dunes |
| Little Cobb | Sparse grassland; erosion- and overwash-influenced |
| Wreck | Dense <i>Ammophila breviligulata</i> grassland and dunes |
| Ship Shoal | North: salt marsh; overwash-influenced beach South: dense mesic <i>S. patens</i> grassland; salt marsh |
| Godwin | Salt marsh |
| Myrtle | Dense <i>A. breviligulata</i> foredune-grassland |
| Mink | Salt marsh; dense <i>S. patens</i> grassland |
| Smith | North: sparse grassland; overwash- and inlet-influenced South: dune ridges with shrub thickets and pine-hardwood forest, alternating with brackish marshes |

A total of 19 shrub species were found on 13 islands. *Baccharis halimifolia* and *Iva frutescens* occurred on 13 islands, *Borrichia frutescens* on 12, *Myrica cerifera* and *M. pensylvanica* on 11, and each of the other 14 species on four or fewer islands; nine shrub species were found on only one island. The most commonly encountered shrubs were those associated with upper marsh borders (*Baccharis halimifolia*, *Borrichia frutescens*, and *I. frutescens*) and that found in interior uplands (*M. cerifera*). As indicated below, at least four shrub species were considered to have been planted on one or more islands.

Smith Island had particularly high diversity of woody species. Twenty-one of the total 24 tree species were observed on Smith Island, including 14 that were observed nowhere else; no other island had more than 11 total (Parramore Island) or one unique (Cedar Island) tree species. Similarly, 13 of the total of 19 shrub species were observed on Smith Island, including six that were observed nowhere

else; no other island had more than 10 total or two unique species of shrubs (Hog Island).

Ferns occurred only on three large islands. A small group of *Asplenium platyneuron* occurred in a pine-hardwood forest on the central-western portion of Parramore Island. *Osmunda regalis* var. *spectabilis* was rare in the low shrub thicket of central Cobb Island, and was found occasionally in tall thickets on Smith Island. *Thelypteris palustris*, *Pteridium aquilinum*, and *Woodwardia areolata* occurred occasionally in wooded communities on Smith Island. *P. aquilinum* also occurred in dense grassland and foredune communities.

The 217 species and varieties observed included two species at or near the northern limit of their geographic ranges (*Crataegus viridis* and *Quercus virginiana* on Smith Island), six northern outliers, three coastal plain outliers, and one species at its southern coastal limit (*Aristida tuberculosa* on Parramore Island, Table 2). *Quercus virginiana* on Smith Island was perhaps the most conspicuous species at its northern limit.

Six planted species were found on Cedar, Revel, Hog, and Smith Islands, and are likely to be remnants of earlier human habitation. *Euonymus japonica*, *Ficus carica*, *Maclura pomifera*, *Prunus maritima*, *Rubus* spp. and *Salix nigra* (growing with *M. pomifera*) are considered to have been planted because of their association with former building sites.

Twenty-three naturalized species (Fernald 1950) were found on 15 islands (Table 3). *Populus alba* and *Paulownia tomentosa* are considered to be naturalized species because their occurrence lacked direct association with habitation. The occurrence of *Bassia hirsuta* in salt marshes and the occurrence of *Xanthium strumarium* and *Salsola kali* on beaches suggest dispersal by tidal water. Most of the other naturalized species are herbs or grasses. Their presence does not necessarily correlate with high grazing use or human occupation. For example, the historical record does not reflect high human or grazing use of Wreck Island, yet Wreck Island had only one fewer naturalized species than Hog Island which received heavy use. Conversely, Revel Island had both grazing and some occupation, yet only one naturalized species was found.

The total number of species observed ranged from one on Godwin Island to 140 on Smith Island. The greatest number of taxa occurred on Smith (140), Parramore (122), and Hog (102) Islands. Taxa unique to that island comprised 24% of the species observed on Smith Island and 18% of those observed on Parramore Island. The average number of species observed was 99 for those islands which support pine-hardwood forest or tall shrub thickets (Parramore, Revel, Hog, and Smith Islands), 54 for the grassland islands (Rogue, Cobb, Wreck, Ship Shoal, and Myrtle Islands), 35 on low-lying islands subject to frequent flooding and overwash (Metompkin, Cedar, Crescent, and Little Cobb Islands), and 21 on the marsh islands (Chimney Pole Marsh, Godwin Island and Mink Island). There are conspicuous exceptions to the trend in increasing species diversity with increasing structural complexity. For example, only 33 species were recorded on Revel Island (forest), while 84 were recorded on Cobb Island (grassland).

TABLE 2. Vascular plant species observed at the extremes of their geographical ranges on Virginia barrier and marsh islands. Range limits include at or near northern limit (NL), northern outlier (NO), coastal outlier (CO), and at or near southern limit (SL).

| Extreme | Species | Island(s) |
|---------|---|----------------------------|
| NL | <i>Crataegus viridis</i> | Smith |
| NL | <i>Linum virginianum</i> | Hog, Smith |
| NO | <i>Gnaphalium chilense</i> | Wreck, Smith |
| NO | <i>Hypericum hypericoides</i> | Parramore, Cobb |
| NO | <i>Ilex vomitoria</i> var. <i>floridanum</i> | Revel, Smith |
| NO | <i>Quercus virginiana</i> | Smith |
| NO | <i>Physalis viscosa</i> ssp. <i>maritima</i> | Rogue, Myrtle, Mink, Smith |
| NO | <i>Uniola paniculata</i> | Hog, Smith |
| CO | <i>Veronica serpyllifolia</i> | Parramore |
| CO | <i>Danthonia compressa</i> | Parramore |
| CO | <i>Eleocharis erythropoda</i> | Cobb |
| CO/SL | <i>Aristida tuberculosa</i> | Parramore |

DISCUSSION

The species numbers reported here for Parramore (122) and Smith (140) Islands are substantially higher than the 33 and 61 species reported for these same islands by Harvill (1965) and Clovis (1968), respectively. Most species reported by these authors were found also in 1975, although 16 herbaceous species reported by Clovis (1968) were not recorded. By comparison with the numbers of species reported for Assateague (562; Hill 1986), Wallops (488; Klotz 1986), and Fishermans (139; Boulé 1979) Islands, it is apparent that the species lists included here are incomplete and preliminary. It is expected that additional research will expand these lists considerably, particularly for herbaceous species.

There was a notable lack of *Hudsonia tomentosa* which is known from as far south as Nags Head, North Carolina. Klotz (1986) reported this species from two secondary dune sites on Wallops Island, and Higgins et al. (1971) found a small stand on one dune transect on Assateague Island. *Iva imbricata*, a foredune species of the North Carolina barrier islands, apparently does not occur north of the Chesapeake Bay.

The high diversity of woody plant species on Smith Island requires comment. It is impossible to evaluate the effects of human activities or fire history on the composition of this woody flora. It seems likely, however, that the dispersal of plant propagules by birds has had a measurable influence on this flora. Smith Island is at the southern end of the Delmarva Peninsula, an important staging area for migratory birds preparing to cross the mouth of the Chesapeake Bay in their flight

TABLE 3. Naturalized plant species observed (X) on 15 Virginia barrier and marsh islands in 1975. Total number of naturalized species per island is given (Metompkin-ME, Cedar-CE, Parramore-PA, Revel-RE, Crescent-CR, Chimney Pole-CP, Hog-HO, Rogue-RO, Cobb-CO, Little Cob-LC, Wreck-WR, Ship Shoal-SS, Murtle-My, Mink-MI, Smith-SM), along with the number of islands (N) on which each species occurred.

| Species | ME | CE | PA | RE | CR | CP | HO | RO | CO | LC | WR | SS | MY | MI | SM | N |
|---------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Achillea millefolium</i> | . | X | X | . | . | . | X | . | X | . | X | X | X | X | X | 9 |
| <i>Aira elegans</i> | . | . | . | . | . | . | X | . | X | . | . | . | . | . | . | 2 |
| <i>Bassia hirsuta</i> | . | X | X | . | . | . | . | . | X | . | X | . | . | . | . | 4 |
| <i>Centaurium pulchellum</i> | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Cerastium glomeratum</i> | . | X | . | . | . | . | X | X | X | . | X | . | X | . | X | 7 |
| <i>Cynodon dactylon</i> | . | . | X | . | . | . | X | . | . | . | X | . | . | . | . | 3 |
| <i>Chenopodium album</i> | X | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Chenopodium ambrosioides</i> | . | X | . | . | . | . | . | X | X | . | X | X | X | X | X | 8 |
| <i>Eragrostis cilianensis</i> | X | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Paspalum dilatatum</i> | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Paulownia tomentosa</i> | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| <i>Phragmites communis</i> | X | X | X | . | . | . | . | . | X | . | X | X | X | . | X | 8 |
| <i>Poa annua</i> | . | X | . | . | . | . | X | . | . | . | . | . | . | . | X | 3 |
| <i>Polypogon monspeliensis</i> | . | . | X | . | . | . | X | . | . | . | . | . | . | . | X | 3 |
| <i>Populus alba</i> | . | . | X | . | . | . | . | . | . | . | . | . | . | X | . | 2 |
| <i>Rumex acetosella</i> | . | X | X | X | . | . | X | X | X | . | . | . | . | . | X | 7 |
| <i>Rumex crispus</i> | . | . | . | . | . | . | . | . | X | . | X | . | . | X | . | 3 |
| <i>Sonchus asper</i> | . | X | . | . | . | . | X | . | X | . | X | . | . | . | X | 5 |
| <i>Spergularia marina</i> | X | X | . | . | X | X | X | X | . | . | . | X | . | . | . | 7 |
| <i>Verbascum thapsus</i> | . | . | X | . | . | . | X | . | . | . | . | . | . | . | X | 3 |
| <i>Veronica serpyllifolia</i> | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Salsola kali</i> | X | X | X | . | . | . | X | . | X | X | X | . | X | X | X | 10 |
| <i>Xanthium strumarium</i> | X | X | . | . | . | . | . | . | . | . | . | X | X | X | X | 6 |
| Naturalized species | 6 | 11 | 12 | 1 | 1 | 1 | 11 | 4 | 10 | 1 | 9 | 5 | 6 | 6 | 12 | |

south along the Atlantic flyway. The islands are an important part of the flyway (J. M. Hill, unpubl.), and Smith Island may be particularly important as a staging point. The flora of Smith Island may, therefore, receive a relatively heavy "seed rain" of bird-dispersed plant propagules.

Future floristic surveys of these islands should provide interesting information on species richness, similarities and differences among islands of similar physical characteristics and human activity. Such surveys should be designed to reveal patterns of change in species composition through disturbance and succession in a mild storm climate (McCaffrey and Dueser, 1990).

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APPENDIX 1. Vascular plant species observed (X) on 15 Virginia barrier and marsh islands (Metomkin-ME, Cedar-CE, Parramore-PA, Revel-RE, Crescent-CR, Chimney Pole-CP, Hog-HO, Rogue-RO, Cobb-CO, Little Cob-LC, Wreck-WR, Ship Shoal-SS, Mtrtle-My, Mink-MI, Smith-SM) in 1975. Only *Spartina alterniflora* was observed on a sixteenth island, Godwin Island. Number of species per island is given, along with the number of islands (N) on which each species occurred.

| Species | ME | CE | PA | RE | CR | CP | HO | RO | CO | LC | WR | SS | MY | MI | SM | N |
|---------------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| PTERIDOPITYTES | | | | | | | | | | | | | | | | |
| ASPIDACEAE | | | | | | | | | | | | | | | | |
| <i>Thelypteris palustris</i> Schott | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| ASPLENIACEAE | | | | | | | | | | | | | | | | |
| <i>Asplenium platyneuron</i> (L.) | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| Oakes | | | | | | | | | | | | | | | | |
| BLECHNACEAE | | | | | | | | | | | | | | | | |
| <i>Woodwardia areolata</i> (L.) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| Moore | | | | | | | | | | | | | | | | |
| OSMUNDACEAE | | | | | | | | | | | | | | | | |
| <i>Osmunda regalis</i> | . | . | . | . | . | . | . | . | X | . | . | . | . | . | X | 2 |
| var. <i>spectabilis</i> (Willd.) Gray | | | | | | | | | | | | | | | | |
| PTERIDACEAE | | | | | | | | | | | | | | | | |
| <i>Pteridium aquilinum</i> (L.) Kuhn | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| GYMNOSPERMS | | | | | | | | | | | | | | | | |
| CUPRESSACEAE | | | | | | | | | | | | | | | | |
| <i>Juniperus virginiana</i> L. | . | X | X | X | . | X | X | X | . | . | X | X | . | X | X | 10 |
| PINACEAE | | | | | | | | | | | | | | | | |
| <i>Pinus taeda</i> L. | . | X | X | X | . | . | X | . | X | . | . | . | . | . | X | 6 |
| ANGIOSPERMS | | | | | | | | | | | | | | | | |
| ACERACEAE | | | | | | | | | | | | | | | | |
| <i>Acer rubrum</i> L. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | X | 2 |
| AIZOACEAE | | | | | | | | | | | | | | | | |
| <i>Mollugo verticillata</i> L. | X | . | . | . | . | . | . | . | X | . | . | . | . | . | . | 2 |

[illegible]

| Species | ME | CE | PA | RE | CR | CP | HO | RO | CO | LC | WR | SS | MY | MI | SM | N |
|--|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Chenopodium ambrosioides</i> L. | . | X | . | . | . | . | . | X | X | . | X | X | X | X | X | 8 |
| <i>Salicornia bigelovii</i> Torrey | X | X | X | . | . | . | X | . | X | . | X | . | X | X | X | 9 |
| <i>Salicornia europaea</i> L. | X | X | X | . | . | . | . | . | X | . | X | X | . | X | X | 8 |
| <i>Salicornia virginica</i> L. | X | X | X | X | X | X | X | X | X | . | X | X | X | X | X | 14 |
| <i>Salsola kali</i> L. | X | X | X | . | . | . | X | . | X | X | X | . | X | X | X | 10 |
| <i>Suaeda linearis</i> (Ell.) Moq. | X | X | . | . | . | X | . | . | . | . | X | X | X | . | X | 7 |
| CISTACEAE | | | | | | | | | | | | | | | | |
| <i>Helianthemum canadense</i> (L.) Michx. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| CONVOLVULACEAE | | | | | | | | | | | | | | | | |
| <i>Calystegia sepium</i> (L.) R. Br. | X | X | X | . | . | X | X | X | X | . | X | X | X | X | X | 12 |
| CYPERACEAE | | | | | | | | | | | | | | | | |
| <i>Bulbostylis capillaris</i> (L.) C.B. Clarke | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Carex festucacea</i> Schkuhr | . | X | X | . | . | . | X | . | X | . | X | . | . | . | X | 6 |
| <i>Carex pensylvanica</i> Lam. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Carex vulpinoidea</i> Michx. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Cyperus esculentus</i> L. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Cyperus grayi</i> Torrey | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Cyperus odoratus</i> L. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Eleocharis acicularis</i> (L.) R. & S. | . | . | X | . | . | . | . | . | X | . | . | . | . | . | X | 3 |
| <i>Eleocharis erythropoda</i> Steudel | . | . | . | . | . | . | . | . | X | . | . | . | . | . | . | 1 |
| <i>Eleocharis palustris</i> (L.) R. & S. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Eleocharis parvula</i> (R. & S.) Link | . | . | . | . | . | . | X | . | . | . | . | . | . | . | . | 1 |
| <i>Eleocharis tenuis</i> (Willd.) Schultes | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| <i>Fimbristylis spadiacea</i> (L.) Vahl | X | X | X | X | . | . | X | . | X | . | X | X | X | X | X | 11 |

| Species | ME | CE | PA | RE | CR | CP | HO | RO | CO | LC | WR | SS | MY | MI | SM | N |
|--|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|
| <i>Sabatia stellaris</i> Pursh | . | . | . | X | . | . | X | . | . | . | . | . | . | . | X | 3 |
| <i>Centaurium pulchellum</i> (Swartz) | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| Druce | | | | | | | | | | | | | | | | |
| GERANIACEAE | | | | | | | | | | | | | | | | |
| <i>Geranium carolinianum</i> L. | . | . | . | . | . | . | X | . | . | . | . | . | . | . | . | 1 |
| HAMAMELIDACEAE | | | | | | | | | | | | | | | | |
| <i>Liquidambar styraciflua</i> L. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | X | 2 |
| HYPERICACEAE (GUTTIFERAE) | | | | | | | | | | | | | | | | |
| <i>Hypericum gentianoides</i> (L.) BSP. | . | . | X | . | . | . | X | . | X | . | . | . | . | . | . | 3 |
| <i>Hypericum hypericoides</i> (L.) | . | . | X | . | . | . | . | . | X | . | . | . | . | . | . | 2 |
| Crantz | | | | | | | | | | | | | | | | |
| IRIDACEAE | | | | | | | | | | | | | | | | |
| <i>Sisyrinchium angustifolium</i> Miller | . | . | X | . | . | . | . | . | X | . | . | . | . | . | . | 2 |
| JUNCACEAE | | | | | | | | | | | | | | | | |
| <i>Juncus acuminatus</i> Michx. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Juncus biflorus</i> Ell. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| <i>Juncus bufonius</i> L. | . | X | X | . | . | . | X | . | . | . | . | . | . | . | . | 3 |
| <i>Juncus coriaceus</i> Mackenzie | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Juncus debilis</i> Gray | . | . | . | . | . | . | . | . | X | . | . | . | . | . | . | 1 |
| <i>Juncus dichotomus</i> Ell. | . | X | X | . | . | . | X | . | X | . | X | . | . | . | X | 6 |
| <i>Juncus gerardi</i> Loisel. | . | X | X | . | . | . | . | . | . | . | . | . | . | . | . | 2 |
| <i>Juncus roemerianus</i> Scheele | . | X | X | X | . | . | . | X | . | . | . | . | . | X | X | 6 |
| <i>Juncus scirpoides</i> Lam. | . | . | X | . | . | . | X | . | X | . | X | . | . | . | . | 4 |
| <i>Juncus tenuis</i> Willd. | X | X | X | . | . | . | X | . | . | . | X | . | . | . | . | 5 |
| LAMIACEAE (LABIATAE) | | | | | | | | | | | | | | | | |
| <i>Monarda punctata</i> L. | . | . | . | . | . | . | . | X | X | . | X | X | . | . | X | 5 |

[illegible]

| Species | ME | CE | PA | RE | CR | CP | HO | RO | CO | LC | WR | SS | MY | MI | SM | N |
|--|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| <i>Eragrostis ciliaris</i> (All.) Lutati | X | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Festuca rubra</i> L. | X | X | X | . | . | . | X | . | X | . | X | X | X | X | X | 10 |
| <i>Festuca sciurea</i> Nuttall | . | X | . | . | . | . | X | . | . | . | . | . | . | . | X | 3 |
| <i>Muhlenbergia capillaris</i> (Lam.) Trinius | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| <i>Panicum amarulum</i> Hitchc. & Chase | . | . | X | . | . | X | . | . | . | . | X | X | X | . | X | 6 |
| <i>Panicum amarum</i> Ell. | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 15 |
| <i>Panicum dichotomiflorum</i> Michx. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Panicum lanuginosum</i> Ell. | . | . | X | X | . | . | . | . | X | . | . | . | . | . | . | 3 |
| <i>Panicum scoparium</i> Lam. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| <i>Panicum sphaerocarpon</i> Ell. | . | . | . | . | . | . | . | . | X | . | . | . | . | . | . | 1 |
| <i>Panicum virgatum</i> L. | X | . | X | . | . | . | X | . | X | . | . | . | . | . | X | 5 |
| <i>Paspalum dilatatum</i> Poiret | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Paspalum floridanum</i> Michx. | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Phragmites communis</i> Trinius | X | X | X | . | . | . | . | . | X | . | X | X | X | . | X | 8 |
| <i>Poa annua</i> L. | . | X | . | . | . | . | X | . | . | . | . | . | . | . | X | 3 |
| <i>Polypogon monspeliensis</i> (L.) Desf. | . | . | X | . | . | . | X | . | . | . | . | . | . | . | X | 3 |
| <i>Puccinellia fasciculata</i> (Torr.) Bicknell | X | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Setaria geniculata</i> (Lam.) Beauvois | . | . | X | X | . | . | X | X | X | . | X | X | X | X | X | 10 |
| <i>Setaria magna</i> Griesbach | . | . | X | . | . | . | . | . | . | . | . | . | . | . | . | 1 |
| <i>Sparina alterniflora</i> Loisel. | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 16 |
| <i>Sparina patens</i> (Ait.) Muhl. | X | X | X | X | X | X | X | X | X | . | X | X | X | X | X | 14 |
| <i>Sphenopholis obtusata</i> (Michx.) Scribner | . | . | . | . | . | . | . | . | X | . | X | . | . | . | . | 2 |

| Species | ME | CE | PA | RE | CR | CP | HO | RO | CO | LC | WR | SS | MY | MI | SM | N |
|--|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|
| <i>Triplasis purpurea</i> (Walt.) Chapman | X | X | X | . | . | . | X | . | X | . | X | . | . | . | X | 7 |
| <i>Uniola laxa</i> (L.) BSP. | . | . | X | . | . | . | X | . | . | . | . | . | . | . | X | 3 |
| <i>Uniola paniculata</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| POLYGONACEAE | | | | | | | | | | | | | | | | |
| <i>Polygonum glaucum</i> Nuttall | . | . | . | . | . | . | X | . | X | . | . | . | . | . | . | 2 |
| <i>Polygonum hydropiperoides</i> Michx. | . | . | X | . | . | . | X | . | . | . | . | . | . | . | . | 2 |
| <i>Rumex acetosella</i> L. | . | X | X | X | . | . | X | X | X | . | . | . | . | . | X | 7 |
| <i>Rumex crispus</i> L. | . | . | . | . | . | . | . | . | X | . | X | . | . | X | . | 3 |
| PRIMULACEAE | | | | | | | | | | | | | | | | |
| <i>Samolus parviflorus</i> Raf. | X | X | X | . | . | . | X | . | X | . | . | . | . | . | X | 6 |
| RHAMNACEAE | | | | | | | | | | | | | | | | |
| <i>Berchemia scandens</i> (Hill) Koch | . | . | X | . | . | . | . | . | . | . | . | . | . | . | X | 2 |
| ROSACEAE | | | | | | | | | | | | | | | | |
| <i>Amelanchier obovalis</i> (Michx.) Ashe | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| <i>Crataegus viridis</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| <i>Prunus maritima</i> Marshall | . | . | . | . | . | . | X | X | . | . | . | . | . | . | . | 2 |
| <i>Prunus serotina</i> Ehr. | . | X | X | . | . | . | X | X | . | . | X | . | . | . | X | 6 |
| <i>Rubus argutus</i> Link | . | X | X | . | . | . | X | . | X | . | . | . | . | . | . | 4 |
| <i>Sorbus arbutifolia</i> (L.) Heyn. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| RUBIACEAE | | | | | | | | | | | | | | | | |
| <i>Diodea virginiana</i> L. | . | . | X | . | . | . | X | . | . | . | . | . | . | . | . | 2 |
| <i>Galium hispidulum</i> Michx. | . | . | . | . | . | . | X | . | . | . | . | . | . | . | X | 2 |
| <i>Galium pilosum</i> Aiton | . | . | . | . | . | . | X | . | . | . | . | . | . | . | . | 1 |
| <i>Galium tinctorium</i> L. | . | . | X | . | . | . | X | . | X | . | . | . | . | . | . | 3 |

| Species | ME | CE | PA | RE | CR | CP | HO | RO | CO | LC | WR | SS | MY | MI | SM | N |
|--|----|----|-----|----|----|----|-----|----|----|----|----|----|----|----|-----|---|
| <i>Boehmeria cylindrica</i> (L.) Swartz | . | . | X | . | . | . | X | . | . | . | . | . | . | . | X | 3 |
| VERBENACEAE | | | | | | | | | | | | | | | | |
| <i>Callicarpa americana</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| <i>Lippia lanceolata</i> Michx. | . | . | X | . | . | . | X | . | . | . | . | . | . | . | . | 2 |
| VITACEAE | | | | | | | | | | | | | | | | |
| <i>Parthenocissus quinque-</i> <i>folia</i> (L.) Planchon | X | X | X | . | . | . | X | . | . | . | . | . | . | . | X | 5 |
| <i>Vitis aestivalis</i> Michx. | . | X | X | . | . | . | X | . | . | . | . | . | . | . | X | 4 |
| <i>Vitis rotundifolia</i> Michx. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| ZOSTERACEAE | | | | | | | | | | | | | | | | |
| <i>Zostera marina</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | X | 1 |
| Species per island | 43 | 77 | 120 | 33 | 12 | 22 | 102 | 38 | 84 | 6 | 68 | 39 | 42 | 38 | 138 | |

Plant Associations on the Virginia Barrier Islands

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ABSTRACT

Vegetation maps (1:20000 scale) and descriptions of plant associations were compiled for 16 barrier and marsh islands on the seaward margin of the Delmarva Peninsula (USA): Metompkin, Cedar, Parramore, Revel, Crescent, Chimney Pole Marsh, Hog, Rogue, Cobb, Little Cobb, Wreck, Ship Shoal, Godwin, Myrtle, Mink and Smith. These maps were based on photointerpretation of false-color infrared aerial photography taken in 1974. Extensive ground-truthing revealed 26 mapping units based on botanical, topographic and edaphic attributes. Each unit represents a distinctive plant association, ecotone or non-vegetated surface. Most associations exhibit relatively low plant species diversity, high consistency in species composition and strong dominance by one or a few plant species. Variation among communities reflects the effects of location, topography, edaphic factors, consumer influence and disturbance history. With periodic resurvey, these maps will be useful for describing site-specific vegetation dynamics and succession on this rapidly-changing landscape.

Key Words: barrier island, Delmarva Peninsula, landscape, plant association, succession, vegetation

INTRODUCTION

The islands located on the seaward margin of the southern Delmarva Peninsula (USA) are among the least disturbed and most dynamic coastal landscapes remaining in North America (Hayden *et al.*, in press). Although relatively free of recent human activity, these islands are subject to the effects of recurrent coastal storms (Dolan *et al.*, 1988), the continuing secular rise in sea level (Aubrey and Emery 1983), and the effects of landward migration across the coastal margin (Dolan *et al.*, 1979). These islands thus offer the potential to study the ecosystem effects of climate change and climate variation on a coastal system that is relatively free from the effects of other, confounding sources of influence. As background for such studies, McCaffrey (1975, 1976) prepared vegetation maps and accompanying descriptions of plant associations for 16 barrier and marsh islands in 1975.

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The present paper describes these plant associations and presents detailed (1:20000 scale) vegetation maps. This information provides an historical baseline for studies of vegetation change and landscape dynamics in this rapidly-changing coastal environment. This paper and the attached maps are a companion to the floristic information reported by McCaffrey and Dueser (1990)

STUDY AREA

The 16 islands are, from north to south: Metompkin, Cedar, Parramore, Revel, Crescent, Chimney Pole Marsh, Hog, Rogue, Cobb, Little Cobb, Wreck, Ship Shoal, Godwin, Myrtle, Mink and Smith (Fig. 1). These islands are centered on latitude $37^{\circ} 30'$ north and longitude $75^{\circ} 40'$ west. With the exception of Wreck Island, which is owned by the Commonwealth of Virginia, most of the acreage of these islands is owned The Nature Conservancy and managed as the Virginia Coast Reserve. This region comprises one of the last stretches of undeveloped coastline on the mid-Atlantic seaboard. Graham (1976) and McCaffrey and Dueser (1990) discuss pertinent aspects of the history of the study area.

METHODS AND MATERIALS

Vegetation maps were prepared from 1:20000-scale false-color aerial infrared transparencies (cf. Holman 1974). The photography was flown by the National Aeronautics and Space Administration, Wallops Island, Virginia during the late morning of June 4, 1974, at 2-2.5 hours before low tide (Roll W 2710101, frames 83-127).

Variation within and between plant associations was identified in the transparencies from different tones and textures of red and black. Non-vegetated features such as open water, submerged sand and mudflats also were delineated. Vegetated and non-vegetated features are referred to collectively as "mapping units." Distinctions between units were based on species composition, growth form, leaf and stem density, tidal influence, substrate mobility, elevation and soil type. Narrow ecotones and small patches of "included" associations were visible in the photography, but were combined with the most similar adjacent mapping unit.

Field maps at 1:6500 scale were prepared by magnifying the transparencies using a reflecting projector. Differences in photo-appearance were traced onto acetate overlays and labeled with preliminary mapping unit interpretations. Blueprints of these overlays were field-checked in 43 days between early March and late July, 1975. Variations in photo-appearance portrayed on the field maps were inspected along multiple transects across and along each island. At several stops in each preliminary mapping unit, a number was recorded on the map and keyed to a brief site description. Each description included percent cover (visual estimation), species relative abundances, canopy height and relative leaf or stem density, salinity and edaphic factors, topography, dune height and other observations.

Relative abundances of conspicuous species were estimated visually as follows: Dominant - most abundant plant species characterizing the mapping unit; Abundant - plants found in quantity essentially throughout the mapping unit; Frequent - plants scattered throughout the mapping unit; and Occasional - individuals or colonies observed infrequently and usually noted simply as "present" in a unit. Characteristic species composition and relative abundances for each mapping unit

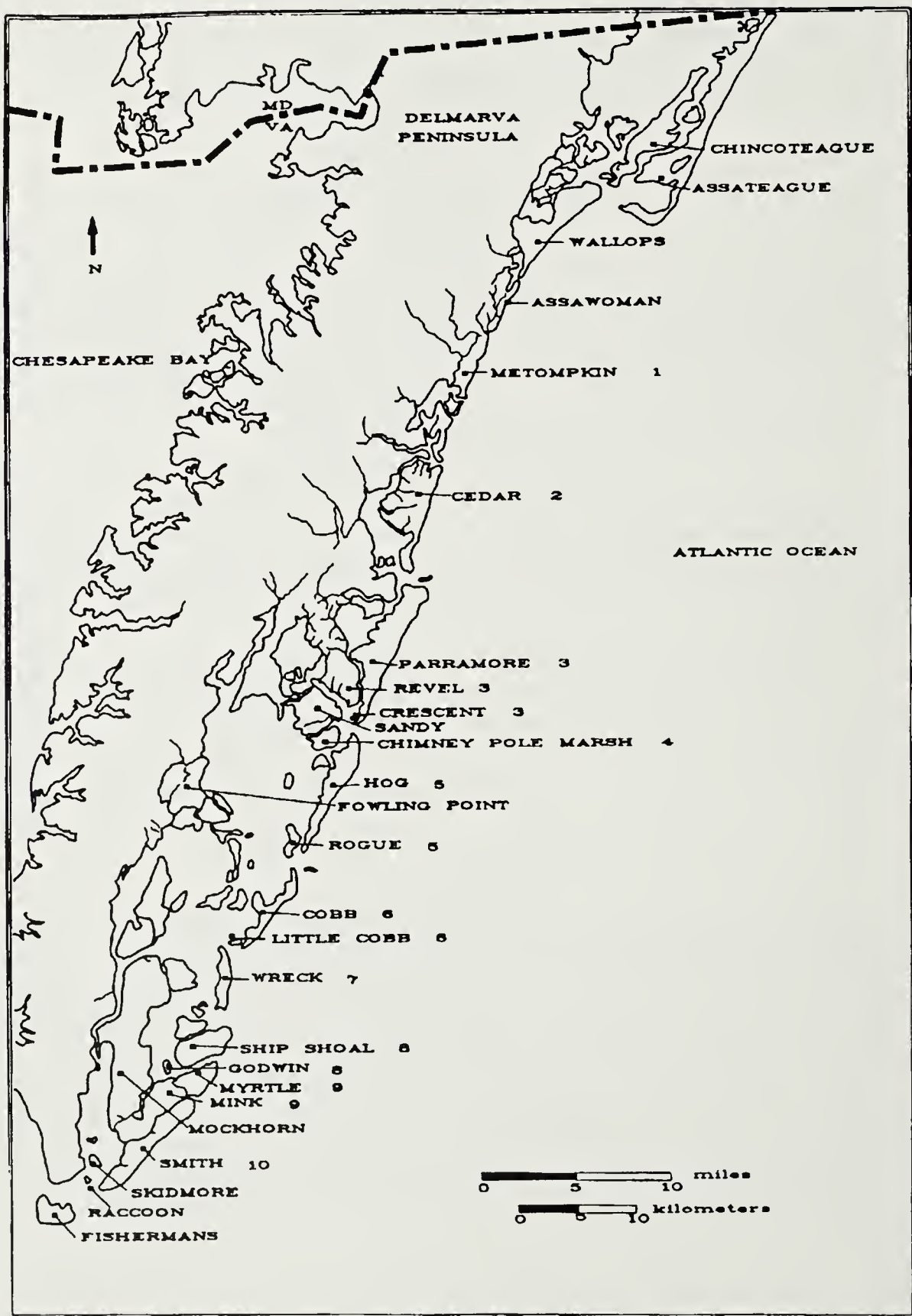


FIGURE 1. The Virginia barrier islands extend the length of the seaward margin of the southern Delmarva Peninsula. Number after island name refers to vegetation map for that island.

are indicated below and in Appendix 1. Relative abundances of species in each mapping unit on each island are available from the second author upon request.

Field data formed the basis for revised photointerpretation, for written descriptions of mapping units, and for description of variations among units and islands. Final photointerpretation was recorded on acetate overlays directly from the 1:20000-scale transparencies. Minimum mapping unit size was determined by the smallest area which could be enclosed by a "00" drafting pen, approximately 30 x 30 m on the ground. Extreme portions of some islands were not covered by the photographs. To complete the bayshore outline of the salt marsh west of Cedar Island, the northeastern beach and bayshore salt marsh of Parramore Island, and the western sides of Godwin and Mink Islands, the maps published here were prepared by merging the vegetation photo-interpretation with the water boundary shown on island basemaps provided by The Nature Conservancy (Dueser *et al.*, 1976).

MAPPING UNIT DESCRIPTIONS

Twenty-six mapping units were identified. These included sparsely vegetated sand and salt flats; sparse and dense grasslands; shrub thickets; upland forests of pine and hardwood species; fresh, brackish and salt marshes; and a variety of unvegetated surfaces. The characteristic plant species for each mapping unit are listed in Appendix 1. Conspicuous inter-island variation in the composition of plant associations is discussed below. Inter-island variation in the number and types of plant associations is illustrated on the attached vegetation maps: Map 1 (Metompkin), Map 2 (Cedar), Map 3 (Parramore, Revel and Crescent), Map 4 (Chimney Pole Marsh), Map 5 (Hog and Rogue), Map 6 (Cobb and Little Cobb), Map 7 (Wreck), Map 8 (Ship Shoal and Godwin), Map 9 (Myrtle and Mink), and Map 10 (Smith).

1) Xeric-Mesic Herbaceous Mapping Units

Herbaceous associations dominated by *Ammophila breviligulata* or *Spartina patens* on xeric or mesic soils are found in the seaward and interior portions of the islands. These units are separated by location, origin, topographic position, species composition and plant density.

Foredune Grassland (A). Xeric foredunes 0.6-1.8 m high parallel the upper beach on most islands, and are sparsely vegetated (5-20% cover) with *A. breviligulata*. In some locations this grassland extends inland into mesic interdunal swales densely vegetated (75-100% cover) with *A. breviligulata* mixed with *S. patens*, *Panicum amarum* and *Strophostyles helvola*. Swale grasslands behind foredunes breached by overwash typically have less than 20% cover. This unit occasionally includes small patches of *Juncus roemerianus* and *Phragmites communis*, as well as scattered small shrubs and vines.

Sparse Grassland (g). Dry, sandy grassland with 5-20% cover occurs above the upper beach on overwash areas having a surface of shell material. Dominant species include *A. breviligulata*, *Cakile edentula*, and *Spartina patens* or *Solidago sempervirens*. Dunes up to 0.6 m high and intermittent foredunes protecting small areas of denser grassland occur in this unit. On the lee side of the southern end of Smith Island the sparse grassland occurs at 1.5-2.4 m in elevation above the surrounding surface, and is dominated by *Andropogon scoparius*, *S. sempervirens*,

moss and scattered *Myrica cerifera*. Sparse grassland typifies Metompkin Island and the narrow, low-lying portions of several other islands.

Foredune-Sparse Grassland Complex (Ag). *Ammophila breviligulata* foredunes, 1.2-3.0 m in elevation above the surrounding surface, and sparse grassland often are interspersed and inseparable. This unit occurs primarily on narrow, overwash-influenced islands such as Metompkin, Cedar and the northern end of Smith Island.

Open Dunes-Thicket Complex (At). This interior unit is sparsely vegetated (10-50% cover) with grasses (particularly *A. breviligulata*), forbs, and scattered shrubs and small trees. In places there are *M. cerifera* thickets and extensive non-vegetated dunes ("blowouts"). This association occurs only on Revel Island and on the northern end and one-third of the eastern length of Parramore Island. It was mapped as part of the dominant woody vegetation on tops of the "Parramore Mounds" (i.e., scattered low, sandy interior dunes on Parramore Island).

Beach (B). The tidal margin of the ocean beach is non-vegetated. The beach above the berm is sparsely vegetated (0-10% cover) with *A. breviligulata*, *C. edentula* and other herbaceous species, and includes scattered low (1.2 m) primary dunes and drift material. Beach accretion is evident on the northern ends of Hog, Cobb, Myrtle and Ship Shoal Islands and on the southern end of Parramore Island. On the eroding northern ends of Cedar and Parramore Islands, storm overwash has penetrated into woody plant associations, leaving dead shrubs and trees on the beach.

Dense Grassland (G). Dense grassland (50-100% cover) is dominated by erect *Spartina patens* with numerous other herbaceous species. *Ammophila breviligulata* is a frequent component. This unit usually occurs in the interior or bayshore portions of the islands. Its several forms include disturbed areas (e.g., lawns of U.S. Coast Guard facilities); xeric or mesic areas with flat or rolling topography and vegetation transitional to thicket (0-50% shrub cover); flat, mesic grassland with tall, erect *S. patens* between foredunes and salt marshes; drift line and *Iva frutescens* borders between brackish and salt marshes and adjacent narrow foredunes or patches of sparse grassland too small to map. Mesic grasslands characterize Hog, Cobb, Wreck and Ship Shoal Islands, whereas dense grasslands on Smith Island are on xeric dune ridges. Ponds of water on Cobb Island and salt flats on Hog Island are notable inclusions in this mapping unit.

Beachgrass Dunes-Dense Grassland Complex (AG). *Ammophila breviligulata* dunes alternate with and often are inseparable from dense *S. patens* grasslands. Beachgrass dunes are taller (0.3-3.0 m) and more densely vegetated (10-50% cover) than is typical, and *Andropogon scoparius* is more abundant. Dense grassland is usually mesic and includes species characteristic of moist sites (*Fimbristylis spadicea*, *Scirpus americanus*, *Juncus* spp.). This unit occurs on Revel, Hog and Cobb Islands. On Hog Island, it includes small salt flats in various stages of succession.

2) Woody Mapping Units

Associations characterized by the occurrence of shrub or tree species usually occupy upland locations. Where beach erosion is pronounced, woody associations occur adjacent to the seaside beach. Shrub associations are dominated by

M. cerifera. Forests vary among islands, but generally are composed of *Juniperus virginiana*, *M. cerifera*, *Persea palustris*, *Pinus taeda* and *Prunus serotina*. Woody units are distinguished by vegetation height and species composition.

An unusual arrangement of scattered low dunes occurs on the central third of Parramore Island and on northern Cedar Island. The "Parramore Mounds" vary in diameter from 7.6-61.0 m and are elevated less than 1.5 m above the surrounding marsh. Vegetation varies in concentric bands from brackish marsh on the periphery to low thicket, to tall thicket, to pine or pine-hardwood forest on the interior. The apex is open sand (0-15% cover), with trees, shrubs and grasses similar to the open dunes-thicket complex of northern Parramore Island.

Tall Thicket (T). Impenetrable *M. cerifera* greater than 3.0 m tall dominate elevated portions of several islands. The canopy is closed, producing a dense herbaceous layer composed chiefly of lianas. There is dense herbaceous ground cover on mesic sites with an open canopy. Thickets are shorter in stature along the borders of fresh, brackish and salt marshes, and *M. cerifera* is replaced here by *Baccharis halimifolia* and *I. frutescens*, with herbaceous species characteristic of the adjacent association.

On Cedar Island *M. pensylvanica* is more abundant than *M. cerifera*. *Rhus radicans* and *Parthenocissus quinquefolia* are abundant on thicket edges. In the hardwood forest of Parramore Island, *Persea palustris* gradually declines in stature toward the edge of the unit and is mixed with tall (4.6 m) *M. cerifera* and scattered pines and cedars, creating an unusual tall thicket composition. Tall thickets on parallel secondary dune ridges on southern Smith Island have *M. cerifera* interspersed with *Smilax bona-nox* and *R. radicans*. *Ilex vomitoria*, near the northern end of its range, is frequent on Smith Island, but *J. virginiana* occurs very infrequently. The only insular location of *Quercus virginicus* is in a tall thicket near Smith Island beach.

Open Dunes-Tall Thicket Complex (AT). Large patches of tall (3.0-4.6 m) *M. cerifera* thicket alternate with open, sparsely vegetated dunes along the bayshore marshes on the northern end of Hog Island. This unit has the composition of typical tall thicket (T). The dune portion (A) of the complex has sparse herbaceous vegetation (5-20% cover) dominated by *A. breviligulata*. Livestock grazed this island, resulting in thickets relatively clear of dead branches and with dense, varied and well-cropped herbaceous vegetation.

Low Thickets (t). Dense stands of *Iva frutescens*, *B. halimifolia* and *M. cerifera* less than 3.0 m tall are typical components, with occasional *J. virginiana*. *Spartina patens* is the usual herbaceous component. This unit includes patches of shrubs in marshes and grasslands having greater than 50% shrub cover. Low thicket varies in species composition, plant density and edge. Where it grades into taller woody units, and in areas subject to occasional flooding, low thicket may have 100% canopy closure. Dense *I. frutescens* 1.0-1.2 m tall, with *S. patens* and *Borrichia frutescens*, form low thickets on sand or drift deposits perched above normal high tide within brackish and salt marshes.

Living shrubs near the ocean are 1.2-2.4 m tall and exhibit the effects of salt-pruning. In places on Cedar, Parramore and Ship Shoal Islands, the seaward edge of low thicket is subjected to erosion, overwash and salt-water flooding, leaving only dead shrubs and trees with an understory of herbaceous dune species.

Myrica pensylvanica and *M. cerifera* are co-dominants with an unusually high abundance of *R. radicans* in low thicket on Cedar Island. Low thicket extends the gradient of decline in plant stature at the edge of the hardwood forest on Parramore Island. In other places on Parramore a narrow north-south line of low thicket has grown in an abandoned roadbed. *Quercus falcata*, *Q. nigra* and *Ilex vomitoria* occur occasionally in low thickets on Smith Island. A narrow, unmapped band of low *M. cerifera*, *Baccharis halimifolia* and *Iva frutescens* surrounds the grassland on Mink Island, and with the grassland, is the only upland vegetation on the island.

Juniper Thicket (J). Juniper thickets are dominated by 3.0-4.5 m tall *J. virginiana* with an abundance of shrubs typical of tall thickets (T). On the northern ends of Cedar and Parramore Islands, juniper thicket is separated from bayshore marshes by a narrow band of low shrubs. *M. pensylvanica* is absent, and *M. cerifera*, *R. radicans* and *Parthenocissus quinquefolia* are uncharacteristically sparse in only one patch of juniper thicket isolated in a salt marsh on Cedar Island. Dead junipers occur along the beach of Cedar Island and near the bayshore marshes of Parramore Island. Juniper thicket on the southern end of Revel Island has an open canopy and merges with the adjacent grassland.

Pine Forest (P). *Pinus taeda* forest occurs only on the interior dune ridges of Parramore Island (Italian Ridge). The understory is sparse under the closed pine canopy. *Myrica cerifera* and *Persea palustris*, with a sparse herbaceous layer, occupy canopy gaps. This forest was estimated to be 65-85 years old in 1968 (O'Neal 1969). In 1975, vast areas of pine had been killed by the southern pine bark beetle and by a rising water table. Some logging occurred in the 1960s (Graham 1976). Many of the Parramore Mounds, mentioned above, had pine canopy and *M. cerifera* understory, and were inter-connected by low shrub thickets of *B. halimifolia*, *I. frutescens* and *M. cerifera*.

Hardwood Forest (H). This forest has essentially 100% cover of medium-small hardwood trees or tall shrubs intertwined with lianas forming a dense, nearly impenetrable woodland. This association occurs only on Parramore and Smith Islands, where it often occurs in wet, low-lying locations.

Myrica cerifera, *P. palustris*, *Smilax bona-nox*, *R. radicans* and *Parthenocissus quinquefolia* are the most abundant species. *Juniperus virginiana* is a dominant species on Parramore Island, and *Acer rubrum*, *Ilex* spp., *Liquidambar styraciflua* and *Prunus serotina* occur occasionally. *Prunus serotina* is a dominant component on Smith Island. *Robinia pseudo-acacia* and *I. vomitoria* are abundant on Smith, while *Sassafras albidum*, *J. virginiana*, *L. styraciflua*, *Q. falcata*, *Q. stellata* and *Q. nigra* occur only infrequently. In some locations, as in the southern extension of this unit on Parramore Island, there is a gradual decline in plant stature and canopy closure; the edge of the forest in such locations was mapped as tall thicket.

Pine-Hardwood Forest Complex (PH). Hardwood forest on old dune ridges on Parramore, Revel and Smith Islands includes scattered *Pinus taeda*. *Juniperus virginiana* is more abundant on Revel Island than on the other two islands. Open areas of dead pines and fallen logs have an understory of *M. cerifera*, *Persea palustris*, *Prunus serotina* and, on Smith Island, *I. vomitoria*. Herbaceous components include *Andropogon scoparius*, *A. virginicus*, *Festuca rubra*, *Opuntia com-*

pressa, *Spartina patens* and *Uniola laxa*. The edges of this association grade into pine forest, hardwood forest, tall thicket or marsh.

3) Hydric-Halophytic Herbaceous Mapping Units

Water- or salt-related units include marshes, open water and virtually bare areas affected by storm overwash and occasional tidal flooding. Marsh communities are separated by species composition, topographic position and tidal influence.

Low Salt Marsh (m). Bayshore marshes have 75-100% cover of *S. alterniflora*, frequently with the macroalgae *Ulva lactuca* and *Fucus vesiculosus* also abundant. Although not mapped separately, short (17-25 cm), medium (26-91 cm) and tall (92-167 cm) height classes of *S. alterniflora* were observed. The taller *S. alterniflora* was less dense than the shorter, as has been reported elsewhere by Holman (1974). The daily tidal range of 1.0-1.4 m floods most marsh areas twice a day. Sinuous creeks dissect the marsh surface. Low marsh comprises most of Chimney Pole Marsh and Ship Shoal, Godwin, Myrtle and Mink Islands.

Marsh substrate changes along a gradient from upland to open water. Higher elevations in low marsh usually have firm organic sediments and support short, often dense, *S. alterniflora*. Lower elevations have fine-grained, mucky sediments which are inundated several hours per day and which support tall *S. alterniflora*. Driftlines of *Borrichia frutescens* and *Iva frutescens* usually separate low marsh and upper low marsh from other herbaceous mapping units.

Upper Low Salt Marsh (Mm). A halophytic association (50-100% cover), usually flooded to a depth of < 10 cm, occupies the higher elevations of low marsh. It is dominated by *Salicornia virginica* and short *Spartina alterniflora*, often with a layer of unicellular algae and sulfur bacteria. A border of *Distichlis spicata*, *B. frutescens*, *I. frutescens*, *S. patens* and drift material usually separates it from upland grassland or woody associations. Upper low marsh includes small mudflats, salt flats, salt ponds, *Juncus roemerianus* colonies, drift mats and some scattered elevated patches of shrubs. This mapping unit is referred to by some authors (Levy 1983, Harvill 1965, Clovis 1968) as tidal flats or salt flats with various combinations of dominant species and by other authors (Martin 1959, Higgins *et al.*, 1971, Klotz 1986) as part of the salt marsh.

Brackish Marsh (M). Brackish marsh has 100% cover of dense, typically decumbent, *D. spicata* and *S. patens* with numerous salty-to-brackish pools. This association fringes the edges of salt flats. Salinity varies with the frequency of precipitation and saltwater flooding. Due to the range of salinity, brackish marshes may gradually merge with upper low marsh, fresh marsh or dense grassland. Higher elevations include small areas of shrub thicket, such as on the Parramore Mounds. The presence of *D. spicata*, *S. patens* or *I. frutescens* distinguishes brackish from fresh marsh, and the drift line separates brackish from salt marsh. Dense grassland is usually drier than brackish marsh and has erect *S. patens*.

Salt Flat (s). Salt flats are intermittently flooded areas of firm sand with a high salt concentration and a surface layer of unicellular algae and sulfur bacteria. The edges have less than 15% cover of halophytic species (typically *Salicornia virginica*, *S. bigelovii* and *S. europaea*), with individual plants scattered sparsely elsewhere. Salt flats are differentiated from mud flats and wash flats by the algal layer, a gray-caked surface appearance and the sparse halophytic vegetation. Salt flats are

found on all islands, most commonly associated with former drift mat locations on the upper edge of the upper low marsh.

Fresh Marsh (F). Fresh marsh is dominated by *Spartina patens*, and on Parramore Island, by *Panicum dichotomiflorum* and *Typha angustifolia*. Fresh marshes occupy wet soil or standing fresh-to-slightly brackish water, and often encircle open water. They include scattered *Baccharis halimifolia* and occasional shrub thickets, and they may extend beneath adjacent wooded canopies. Fresh marshes occur only on Parramore, Hog and Smith Islands.

Open Water (w). Ephemeral or permanent ponds with filamentous algae are found on most islands. Those nearest the ocean or creeks are salty, while those further inland are brackish or fresh. They are usually surrounded by a marsh or flooded grassland with *S. patens*, *S. alterniflora* and other species. Halophytic species characteristic of salt flats and upper low marsh surround salt ponds located near low marshes.

4) Other Mapping Units

Several essentially bare or submerged mapping units were recognized on the basis of location, origin, substrate composition and plant species composition.

Drift (dr). Extensive areas of drift material composed chiefly of dead stems of *S. alterniflora* and flotsam are found on the higher elevations of salt marshes, typically bordering grassland. Drift mats are transported by storm tides; their deposition may produce essentially non-vegetated mud flats or salt flats. They are recognized as a unit because of their occasional large area and their role in substrate stabilization and plant propagation. The sparse vegetation associated with the edges of the driftline included *C. edentula*, *Borrichia frutescens*, *Calystegia sepium*, *D. spicata*, *I. frutescens*, *S. patens*, *Solidago sempervirens*, and numerous other species typical of beaches and brackish wetlands.

Submerged Sand (b). Contiguous with some islands are submerged accumulations of sand near a spit or inlet. Under a regime of sediment accretion, submerged sand having primarily oceanic influence may emerge and join an island beach. With accumulation of fine sediments in the lee of an island, and with establishment of *S. alterniflora*, low marshes may develop.

Underwater Flora (or Fauna) (uw). Underwater features that were visible on the aerial photographs include oyster beds, patches of dense algal growth and human artifacts.

Peat Outcrop (Peat). Outcrops of marsh peat are found on seaside and inlet beaches. The outcrops contain roots of *S. alterniflora* and *S. patens*, but occasional *Ulva lactuca* is the only living vegetation. These features change with short-term erosion and storm activity. They are found on Metompkin, the southern end of Cobb, Ship Shoal, Myrtle and Smith Islands.

Wash Flat (wf). Wash flats appear as bayshore beaches. They occur above buried low marsh in overwash areas and in ephemeral inlets. Portions of a wash flat may receive tidal flooding. There is sparse (0-10%) *S. alterniflora* near tidal creeks and elsewhere occasional inclusions of *S. alterniflora* with 10-50% cover and sparse halophytic vegetation. Wash flats may be separated from the ocean by sparse grasslands, or they may be continuous with the beach. This "rear beach" lacks the abundance of shell material found on the ocean beach and sparse

grasslands. Wash flats lack the algae and the salt-caked surface characteristic of salt flats, although wash flats appear to be transitional to salt flats. Wash flats are found primarily on narrow parts of islands such as Crescent Island, southern Hog Island and northern Smith Island.

Mud Flat (mf). Mud flats have a "muddy" surface and little vegetation except for occasional *U. lactuca*, *S. alterniflora* and other halophytes. Mud flats form where there recently was a drift mat (0-20% cover) or where accumulations of fine estuarine sediments accrete onto a marsh. They are successional to salt marsh and occur in three types of locations: as shallowly-flooded extensions of marsh islands, within low marsh or upper low marsh, and as leeward extensions of overwash fans.

DISCUSSION

The surfaces of the islands and marshes are conspicuously patchy, with distinct zonation and sharp transitions between patches. Twenty-six mapping units were identified, including 19 vegetated units. Although the Virginia barrier islands support a rich diversity of plant species (McCaffrey and Dueser 1990), most vegetated units exhibit dominance by only one or a few species:

A, g, Ag, At, B, G, AG - *Ammophila breviligulata*, *Spartina patens*

T, AT - *Myrica cerifera*

t - *Iva frutescens*, *Baccharis halimifolia*, *Myrica cerifera*

J - *Juniperus virginiana*

P - *Pinus taeda*

H - *Myrica cerifera*, *Persea palustris*, *Juniperus virginiana*, *Acer rubrum* (Paramore Island); *Prunus serotina*, *Robinia pseudoacacia*, *Ilex vomitoria* (Smith Island)

PH - *Pinus taeda*, *Juniperus virginiana*, *Myrica cerifera*, *Persea palustris*, *Prunus serotina*, *Ilex vomitoria*

m, Mm, M - *Spartina alterniflora*, *Spartina patens*

s - *Salicornia* spp.

F - *Spartina patens*, *Panicum dichotomiflorum*, *Typha angustifolia*

Altogether, then, fewer than 20 vascular plant species dominate the 19 vegetated units. Only the relatively uncommon hardwood (H) and pine-hardwood (PH) forest units typically exhibit inter-island variation in gross composition and appearance.

In addition to compositional differences, mapping units are distinguished from one another by their physical attributes (e.g., location on the island, topographic position, depth and frequency of salt water flooding). Some units appear to exhibit greater variation (i.e., amplitude) in site attributes than others. For example, pine forest (P) typically occurs on xeric sites and hardwood forest (H) on mesic sites. Low thicket (t), by contrast, occurs in fresh, brackish and saline environments and on xeric, mesic and flooded sites. This unit appears to arise through a variety of successional pathways, including from xeric or mesic grassland, from brackish or fresh marsh, and from heavy drift deposits in saline areas. Variability exhibited by a unit must reflect variability in the requirements and tolerances of its component species.

Boulé (1979) identified 14 "natural communities" on Fishermans Island, at the southern end of the Delmarva Peninsula. He used different terminology to describe these communities, but his botanical and physical descriptions identify 12 synonymies with mapping units described here: pioneer beach (B), foredune (A), low dune (g or Ag), backdune (AG), low marsh (m), high marsh (Mm), upper marsh (M), panne (s), marsh transition (t), thicket (T), woodland (H) and fresh marsh (F). Only Boulé's "old dune" and "dune-marsh boundary" units are not readily identified with one of the units reported here. This cross-classification attests to the regional applicability of the units described here.

The islands discussed here range in area and elevation from 29 ha and 0.9 m (Little Cobb) to 2,197 ha and 9.1 m (Parramore). There is a direct relationship between island area, maximum elevation and vegetation complexity, measured as the observed number of mapping units (Dueser and Brown 1980). Larger islands tend to have a greater variety of plant associations ($r = +0.74$), particularly woody associations ($+0.84$), than smaller islands. Similarly, elevated islands tend to have a greater variety of plant associations ($r = +0.60$), particularly woody associations ($+0.78$), than low-lying islands. These patterns of variation must reflect the greater substrate diversity, the more reliable supply of fresh groundwater, and the reduced frequency of overwash and flooding associated with larger area and higher elevation.

Barrier islands frequently exhibit pronounced shore-parallel zonation of plant associations, from barrier beach to bayshore (Dolan *et al.*, 1973 and references therein). Because of the effects of erosional and accretional processes on the Virginia barrier islands, and because these islands are relatively low-lying (0.9-9.1 m), substantial variation on this pattern is evident. This is particularly well-illustrated on Parramore Island, where several thicket (t, T, At) and forest (H, PH) units occur immediately inland from seaside beach (B), and where brackish marsh (M) occurs adjacent to at least 14 other units, including all eight of the units having a conspicuous woody component. Interspersion of mapping units is the rule rather than the exception on these islands.

The mapping units identified here are subject to change through accretion, deposition, erosion and subsidence. These processes may produce transitions from one type of unit to another. For example, low marsh may eventually become upper low marsh through accretion or deposition, or upper low marsh may become low marsh through erosion or subsidence. Both salt marsh units might become mud flat or wash flat through the effects of deposition or erosion produced by overwash. Similarly, shore-front forest might become shrub thicket, foredune grassland, and eventually even beach, through beach erosion. The superficial simplicity suggested by few-species dominance and sharp zonation belies the actual complexity of the types, frequencies and rates of changes which may occur within mapping units. As in other coastal systems (Tyndall and Levy 1978), plant succession is likely to be both relatively rapid and highly stochastic on the Virginia barrier islands.

A sequence of vegetation maps comparable to those presented here is potentially available through the interpretation of historical (post-1933) aerial photography for the islands. Although these photographs vary in type, quality and resolution, it should be possible to produce a decadal sequence of maps from the

1930s through the 1980s. Such maps would support a "time lapse" study of major surficial and vegetation changes on the islands since the historic storm of 1933. It would be possible, for example, to detect temporal changes which have occurred at selected points on the islands and to estimate the probability of a given mapping unit changing into any of the other units through time (Horn 1976). Presumably, most of the transition probabilities are close to zero, while a few are close to one. Nevertheless, because of the strong interplay between biological and physical processes, it is expected that vegetation dynamics will be quite complex despite the superficial simplicity of vegetation structure.

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APPENDIX 1: Relative abundances of plant species recorded in each of the 26 mapping units described in the text. Abundance classes are D - dominant (most abundant or characteristic species found in unit), A - abundant (occurs in quantity throughout unit), F - frequent (scattered plants occurring regularly throughout unit), and O - occasional (infrequent individuals or groups). Prefix "1" indicates local abundance in a particular portion of a mapping unit. For complex mapping unit, abundance in first unit is indicated above the "/" and abundance in the second is below the "/" Absence in a unit is denoted by "-."

| Plant Species | Xeric-Mesic Herbaceous ¹ | | | | | | | | | | Woody ² | | | | Hydric-Halophytic ³ | | | | | | | | | | Other ⁴ | | | |
|--|-------------------------------------|----|-----|-----|---|-----|-----|-------|-----|----|--------------------|----|----|---|--------------------------------|----|---|----|----|----|---|---|---|---|--------------------|------|----|----|
| | A | | | | | T | | | | | P | | | | m | | | | | w | | | | | dr | | | |
| | g | Ag | At | B | G | AG | dr | | | | AT | t | J | P | H | PH | m | Mm | M | s | F | w | | | uw | Peat | wf | mf |
| <i>Achillea millefolium</i> L. | . | . | . | . | O | . | . | F/F | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Ammophila breviligulata</i> Fernald | D | D | D/A | D/- | A | F | D/- | . | D/- | . | . | . | . | A | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Andropogon scoparius</i> Michx. | . | . | . | . | . | F/- | . | A/- | . | F | IF | IO | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Andropogon virginicus</i> L. | . | . | . | . | F | F/F | . | O A/A | F | IF | IF | IF | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Andropogon virginicus</i> var. abbreviatus (L.) Fern. & Griseb. | . | . | . | . | F | -/F | . | O/A | F | IF | O | IF | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Apocynum cannabinum</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | O | . | . | . | . | . | . | . | . |
| <i>Aristida tuberculosa</i> Nuttall | . | . | A- | . | . | . | . | O/- | . | F | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Atriplex arenaria</i> Nuttall | . | O | F/- | . | O | . | . | . | . | . | . | . | . | . | . | . | . | O | . | O | . | O | . | . | . | . | F | O |
| <i>Atriplex patula</i> L. | . | . | . | . | . | . | F | . | . | . | . | . | . | . | . | . | O | . | . | . | . | O | . | . | . | . | . | . |
| <i>Baccharis halimifolia</i> L. | IO | . | . | . | F | F/F | F | A | -/A | A | . | IA | IA | . | IA | IA | . | IA | . | ID | . | A | . | . | . | . | . | . |
| <i>Bassia hirsuta</i> (L.) Ascherson | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | O | . | O | . | . | . | . | . | . | . | O | . |
| <i>Berchemia scandens</i> (Hill) Koch. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | IF | IA | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Boehmeria cylindrica</i> (L.) Swartz | . | . | . | . | . | . | . | . | . | A | . | . | . | . | . | . | . | . | . | A | . | . | . | . | . | . | . | . |
| <i>Borrichia frutescens</i> (L.) DC. | . | . | . | . | . | . | A | . | . | A | . | . | . | . | . | . | . | A | IA | O | . | A | . | . | . | . | O | A |
| <i>Cakile edentula</i> (Bigel.) Hooker | F | D | A/- | . | D | . | F | . | . | . | . | . | . | . | . | . | . | . | . | . | . | A | . | . | . | . | O | O |
| <i>Calystegia sepium</i> (L.) R.Br. | F | F | -/F | . | . | F | A | F | . | F | . | . | . | . | . | . | . | . | . | . | . | O | . | . | . | . | . | . |
| <i>Campsis radicans</i> (L.) Seemann | . | . | . | . | . | . | . | A | . | . | . | . | . | . | F | F | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Carduus spinosissimus</i> Walter | F | . | . | . | F | F/- | . | F A/A | O | . | O | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Carex festucacea</i> Schkuhr | IO | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | O | . | . | . | . | . | . | . | . |

| | A | g | Ag | At | B | G | AG | dr | T | AT | t | J | P | H | PH | m | Mm | M | s | F | w | dr | b | uw | Peat | wf | mf |
|--|---|---|-----|-----|---|---|-----|----|-----|-----|----|----|----|----|----|----|----|---|---|----|---|----|---|----|------|----|----|
| <i>Juncus roemerianus</i> Scheele | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | F | . | O | . | . | . | . | . | . | . |
| <i>Juncus scirpoides</i> Lam. | O | . | . | IO | . | O | -/O | . | . | F/- | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Juniperus virginiana</i> L. | . | . | . | -/D | . | . | . | . | O | -/O | F | D | F | ID | ID | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Kosteletskyia virginica</i> (L.) Presl | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | F | . | A | O | . | . | . | . | . | . |
| <i>Lepidium virginicum</i> L. | F | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Limonium nashii</i> var. <i>nashii</i> Small | . | . | . | . | . | . | . | F | . | . | . | . | . | . | . | . | . | F | . | F | . | F | . | . | . | . | . |
| <i>Lippia lanceolata</i> Michx. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | A | . | . | . | . | . | . | . |
| <i>Liquidambar styraciflua</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | IO | IO | IF | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Mikania scandens</i> (L.) Willd. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | F | . | F | . | . | . | . | . | . | . |
| <i>Mitchella repens</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | O | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Monarda punctata</i> L. | . | . | . | . | . | O | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Myrica cerifera</i> L. | . | . | . | -/D | . | F | F/F | . | D | -/D | D | A | D | D | D | . | . | . | . | IF | . | . | . | . | . | . | . |
| <i>Myrica pensylvanica</i> Loisel. | . | . | . | -/O | . | . | . | . | IA | . | IA | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Oenothera laciniosa</i> Hill | . | . | . | . | . | O | F/- | . | O | . | IF | O | . | . | F | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Opuntia compressa</i> (Salisbury) Macbride | . | . | . | . | . | . | . | . | O | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Panicum amarulum</i> Hitchc. & Chase | F | . | . | . | . | . | O | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Panicum amarum</i> Ell. | A | O | F/- | . | O | O | . | . | . | . | . | . | . | . | . | . | . | . | . | ID | . | . | . | . | . | . | . |
| <i>Panicum dichotomiflorum</i> Michx. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Panicum virgatum</i> L. | . | . | . | . | . | O | . | . | . | . | . | . | O | . | IA | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Parthenocissus quinquefolia</i> (L.) Planchon | . | . | . | . | . | . | . | . | D | -/A | F | IA | . | A | IA | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Persea palustris</i> (Raf.) Sarg. | . | . | . | -/F | . | . | . | . | . | . | . | IF | D | D | ID | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Phragmites communis</i> Trinius | . | . | . | . | . | . | . | . | . | O | IF | . | . | . | . | . | . | F | . | F | . | . | . | . | . | . | . |
| <i>Pinus taeda</i> L. | . | . | . | -/F | . | . | . | . | O | -/O | IO | D | . | D | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Pluchea purpurascens</i> (Swartz.) DC. | . | . | . | . | . | . | . | . | . | A | . | . | . | . | . | . | . | A | . | A | A | . | . | . | O | . | . |
| <i>Poa annua</i> L. | . | . | . | . | . | . | . | . | -/F | . | . | . | . | ID | ID | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Prunus serotina</i> Ehr. | . | . | . | -/O | . | . | . | F | -/O | . | . | . | . | . | ID | ID | . | . | . | . | . | . | . | . | . | . | . |
| <i>Ptilimnium capillaceum</i> (Michx.) Raf. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | O | . | . | . | . | . | . | . | . |

| | A | g | Ag | At | B | G | AG | dr | T | AT | t | J | P | H | PH | m | Mm | M | s | F | w | dr | b | uw | Peat | wf | mf |
|--------------------------------------|---|---|-----|-----|---|---|----|----|---|-----|---|---|---|----|----|---|----|----|---|----|---|----|---|----|------|----|----|
| <i>Suaeda linearis</i> (Ell.) Moq. | . | . | . | . | . | . | . | F | . | . | . | . | . | . | . | . | O | . | O | . | . | F | . | . | . | F | . |
| <i>Teucrium canadense</i> L. | . | . | . | . | . | F | . | F | . | . | . | . | . | . | . | . | . | . | . | . | . | O | . | . | . | . | . |
| <i>Typha angustifolia</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | IA | . | ID | . | . | . | . | . | . | . |
| <i>Typha latifolia</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | IO | . | . | . | . | . | . | . |
| <i>Uniola laxa</i> (L.) BSP. | . | . | . | . | . | . | . | . | . | . | . | . | A | IF | A | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Vitis aestivalis</i> Michx. | . | . | . | . | . | . | . | . | F | -/F | . | . | A | IF | A | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Vitis rotundifolia</i> Michx. | . | . | . | . | . | . | . | . | . | . | . | . | . | IF | IA | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Xanthium strumarium</i> L. | . | O | -/F | . | O | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | O | . | . | . | . | . |
| <i>Zanthoxylum clava-hercules</i> L. | . | . | . | -/F | . | . | . | . | . | O/- | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| <i>Zostera marina</i> L. | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | IF | . | . | . |

¹Xeric-mesic herbaceous mapping units: A = foredune grassland; g = sparse grassland; Ag = beachgrass dunes-sparse grass-land complex; At = open dunes-thicket complex; B = beach; G = dense grassland; AG = open dunes-dense grassland complex; dr = bayshore drift material deposited on dense grassland.

²Woody mapping units: T = tall thicket; AT = open dunes-tall thicket complex; t = low thicket; J = juniper thicket; P = pine forest; H = hardwood forest; PH = pine-hardwood forest.

³Hydric-halophytic mapping units: m = low salt marsh; Mm = upper low salt marsh; M = brackish marsh; s = salt flat; F = fresh marsh; w = open water.

⁴Other mapping units: dr = drift material deposited on unvegetated surface; b = submerged sand; uw = underwater; peat = peat outcrop; wf = wash flat; mf = mud flat.

Vegetation Dynamics on the Virginia Barrier Islands

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ABSTRACT

The vegetation on the Virginia barrier islands is affected by oceanside erosion and accompanying salt spray which impact strand communities, and by bayside accretion which provides impetus for hydrarch succession. Controlling environmental complexes include: extent of flooding, soil moisture, soil nutrient levels and autogenic factors, as well as salt spray. A variety of vegetation patterns are found on stable dunes, unstable dunes, interdunal depressions, sand flats, relic dunes and bayside sites of various physiographic aspects. Succession can be progressive, retrogressive, chronic-patchy or cyclic. Historic, natural and anthropogenic impacts have disrupted communities and depauperized the flora.

Key words: barrier islands, plant succession, vegetation, strand communities.

INTRODUCTION

The barrier islands are continually subjected to the impacts of longshore currents, tides, waves, and wind. Consequently, shorelines and dunes undergo constant physiographic change which affects their vegetative composition. In addition, long-term transformations are caused by an oceanic rise amounting to about 2 mm/yr in the north near Metomkin Island and about 1.2 mm/yr near Fisherman's Island in the south (Rice, *et al.* 1980). Given a 0.05° beach slope, this seemingly slight rise can produce 2.2 to 1.4 horizontal meters of marine encroachment each year. Simultaneously on the bayside of the barrier islands, accretion is occurring due to wind and water action.

The vegetation of these islands, in addition to wetlands, includes hydric and xeric grasslands, and shrub and tree dominated communities. Local factors such as salt spray, soil salinity, nutrient availability, soil moisture, and time since last significant perturbation influence species' composition and distribution (Wells, 1928; Oosting and Billings, 1942).

Perturbations, both natural and anthropogenic, have had a profound impact on the vegetation in this system. Twelve major summer storms (hurricanes) have affected the system in the past 170 years. Those of 1821, 1857, 1903 and 1933 were especially destructive. In addition, strong winter storms (northeasters) such as those in January 1956, March 1962, and February 1988 have also had strong impact. Anthropogenic affects from the Amerind period to the recent past have produced significant changes, especially on the larger Islands. These impacts have included fire, lumbering, reforestation, farming, building, grazing, and plant and animal introductions. Although most of the introduced animal species have been removed or eradicated and many structures reduced, residual effects still remain (Dueser *et al.*, 1976). The most significant impact of the anthropogenic influences appears to have been quantitative and qualitative floristic depauperization.

PLANT SUCCESSION

The organismic successional concepts of Clements (1916, 1936) and the opposing ideas of Gleason (1926) as well as the many related theories have been extensively reviewed (e.g., Whittaker, 1953). Drury and Nisbet (1973) present a strong case in opposition to the unidirectional facilitated succession associated with Clements and more recent authors (e.g., Odum, 1969). Horn (1976), after a succinct review of the alternative concepts, tersely identifies the conflict, "The idea of a stable community is not general in nature, if indeed it exists." He provides a series of models which have direct application to the interpretation of vegetation dynamics on the Virginia barrier islands. Horn's models include chronic, patchy disturbance. This model describes conditions in areas where frequent disruptions lead to shifting successional patches characterized by a random replacement of opportunistic species of similar tolerance. His second model, obligatory succession is Clements' (1916) organismic succession in which autogenic habitat changes produce a predictable climax via predictable seral stages. Usually the process proceeds from extreme conditions to more mesic ones. This is considered progressive succession. If the reverse is true (i.e., development toward more xeric or hydric states) the sequence is considered retrogressive. Horn's two remaining models are, competitive hierarchy and quasi-reality. In the former, later arriving species out compete earlier ones, but can also invade in their absence. The latter model, quasi-reality, suggests that there is a probability that any species can replace another. However, the probability of each potential replacement varies from species to species. Thus, in the long term vegetation following this model approximates classical organismic succession. In addition, there are numerous examples in the literature of stagnant or cyclic succession (e.g., Watt, 1947; Billings and Moony, 1959).

BARRIER ISLAND SUCCESSION

Wells (1928), Oosting and Billings (1942), Oosting (1945, 1954), Van Der Valk (1974), and Godfrey and Godfrey (1976), among others, have discussed the successional process and various factors which influence it in the North Carolina barrier islands. Dolan *et al.*, (1973) have evaluated human impacts in this system. The floristic complexity of this area has been studied by Hosier and Cleary (1979). In two related studies, Levy (1976) and Harris *et al.*, (1983), the vegetation on the Coastal Engineering Research Center Field Research Facility (CERC) near Duck, North Carolina was described and the changes that occurred over a seven year period documented.

Harvill's (1965) vegetation survey of Parramore Island provided descriptions of the major communities occurring there. In a follow up study, Levy (1983) discussed community dynamics on this island. McCaffrey (1980) included a consideration of vegetation and influencing factors for the whole Virginia barrier island chain in her significant baseline studies. In a related study, Tyndall and Levy (1979) described vegetative dynamics at False Cape in Virginia Beach.

The Virginia barrier islands range from Godwin Island which is completely covered by a cord grass (*Spartina alterniflora*) marsh to Wreck Island which has a dense covering of beach grass (*Ammophila breviligulata*) on the sandy dunes, a low salt marsh, and a central tall bayberry (*Myrica* spp.) thicket. (Taxonomy follows

Radford *et al.*, 1968). The much larger Parramore and Smith Islands, which are physiographically diverse, have correspondingly much greater community diversity.

The habitats on a greatly simplified, highly idealized transect of a typical large island can be identified physiographically and include the foredune, interdunal depressions, sand flats, the rear dune, rear dune troughs, relict dunes and bayside wetlands.

Of great significance throughout this system is a salt spray gradient. During storms, salt spray and accompanying sand scouring can cause significant mortality and necrosis to relatively intolerant species.

The community found on unstable foredunes has been characterized as sparse grasslands (community names generally follow McCaffrey, 1980). These grasslands consist primarily of chronically disturbed patches of beach grass and sea rocket (*Cakile edentula*). Seaside golden rod (*Solidago sempervirens*) is important in some places. The diversity of these communities is far less than similar ones which exist on the Fort Story dunes in Virginia Beach (per. obs.) or at the CERC Research Facility near Duck, N.C. (Harris *et al.*, 1983).

On stable foredunes is found a dense grassland dominated by beach grass. Stability here as elsewhere is only relative and depends upon storm patterns and the impact of long term sea rise. A further analysis of the Duck, North Carolina data of Levy (1976) and Harris *et al.*, (1983), which document the vegetative changes that occurred from 1975-1983, illustrate the dynamic nature of the foredune and adjacent communities. Using Sorenson's (1948) qualitative index of similarity ($IS_s = 2c/a + b$) to compare the earlier results with the later ones, it was found that after seven years the foredune community which was characterized by sea oats (*Uniola paniculata*), beach grass, and sea side goldenrod, had an $IS_s = 50\%$. This difference reflected a loss of two species and a gain of two other species. The adjacent communities, oceanside shrub, a bayberry (*Myrica pensylvanica*) dominated community and oceanside intershrub, a mixed grassland, underwent similar changes during this period. The former had an $IS_s = 33\%$ while the latter had an $IS_s = 30.4\%$. These changes, which were due to the addition of eight new species to each community's flora, document the dynamic nature of vegetation within a degrading zone.

Vegetative shifts similar to those documented for the North Carolina outer banks no doubt also occurred on various portions of the Virginia barrier islands. For example, Levy (1983) notes that on Parramore Island, lines of dead black cherry (*Prunus serotina*) trees some nine meters sea-ward of the summer flood-tide debris are strikingly evident. These trees, which grow a short distance inland with other severely damaged tree species, are interspersed with beach grass. Along the more northern section of this island's beach are lines of dead loblolly pines (*Pinus taeda*), a species which grows further inland where it is protected from salt spray. The rate of ocean incursion is obviously greater here. Since these changes are proceeding from more mesic to more xeric, the process could be described as retrogressive succession in the Clementian sense, however, given the prevailing conditions, Horn's chronic patchy disturbance model would appear to be more appropriate in this case.

The successional patterns in interdunal depressions are more complex. These communities seem to be responding to a soil moisture-flooding gradient (Tyndall and Levy, 1979). Salt spray, however, does play a role here too. Without significant animal impact, an American three square (*Scirpus americanus*) - waterpenny wort (*Hydrocotyl umbellata*) community develops in the deepest, most frequently flooded areas. As these areas fill with wind blown sand and/or organic matter, salt meadow cord grass (*Spartina patens*) first replaces waterpenny wort and ultimately American three square. As conditions become drier and flooding infrequent, little blue stem (*Andropogon virginicus*) dominates. Subsequently a bayberry (*Myrica* spp.) dominated thicket becomes established on the driest sites, often extending on to the rear dune.

Areas impacted by migratory waterfowl have communities dominated by *Centella asiatica* and rushes (*Juncus* spp.) in the wettest, most frequently flooded sites. With decreased frequency of flooding and reduced soil moisture, salt meadow cord grass and American three square replace the rushes. This in turn yields to the bayberry thicket community. Initial pioneers are of course dependent upon existing conditions.

The bayberry thicket serves as a nurse community for black cherry. Ultimately, black cherry can over-top and shade out the bayberry. On sites close enough to the ocean, black cherry eventually grows tall enough to become exposed to salt spray and succumbs. Subsequently, a bayberry thicket is reestablished. Thus, a cyclic succession occurs on these areas.

Where salt spray is not a significant factor, loblolly pine becomes established in areas previously dominated by thicket and black cherry. The pines are followed by oaks (*Quercus* spp.), characteristically live oak (*Q. virginiana*), which appears to represent a climax (i.e., maritime forest). Currently live oak occurs only on Smith Island.

On rear dunes and relict dunes (Parramore Island for example), a nutrient gradient appears to be controlling the successional process. Where nutrient levels are excessively low, loblolly pine appears to replace itself. This is due in part to the depauperate seed rain available. In addition, loblolly pine seems to have a minimal autogenic impact on the soil which is easily eroded by the wind and has a low water holding capacity. The acid pine litter most likely helps to facilitate nutrient leaching. Thus, edaphic and biological conditions on such sites exclude all but those species tolerant of this nutrient poor, xeric, unstable habitat.

If significant amounts of bayberry are established, the cycle may be broken. This species would improve soil nutrient levels (Morris *et al.*, 1974) and thus allow the establishment of other species. Pine litter accumulation could ultimately prevent pine ecesis and lead to soil organic matter increase, thus improving water holding and ion-exchange capacities. Ultimately a maritime forest community might become established.

Sand flats are characterized by very sparse vegetation. Typical species include, beach spurge (*Euphorbia polygonifolia*), sand grass (*Triplasis purpurea*), buttonweed (*Diodia teres*) and evening primrose (*Oenothera humifusa*). Harris *et al.*, (1983) reported that 40% of the sand flat community present on the Duck, North Carolina Research Facility in 1975 had, in seven years, changed to what they called a low dune grass community characterized by the expansion of sand grass and the

invasion and establishment of beach grass, and a few other species. Toward the ocean, oceanside shrub and oceanside intershrub communities evidenced significant expansion into what had been almost barren sand flats. It is likely that similar patterns of succession occur on the Virginia barrier islands as has been reported further south, as the same processes are impacting both areas.

In areas adjacent to the bay classical progressive succession is occurring. The cord grass dominated areas become mixed with salt grass (*Distichlis spicata*), salt meadow cord grass, and rushes. Interspecific competition, fluctuating soil moisture and flooding produce relatively monotypic clumps of these species. As conditions become more mesic, marsh elder (*Iva frutescens*) and groundsel tree (*Baccharis halimifolia*) are established, producing a shrub carr community. Bayberry species form an important component in places.

Further development depends upon physiographic conditions. For example, if conditions become fairly well drained, wax myrtle (*Myrica cerifera*) becomes important and in places is invaded by red cedar (*Juniperus virginia*) followed by the establishment of loblolly pine. A build-up of sand, creating more xeric conditions, could lead to a maritime forest with sassafras (*Sassafras albidum*) and live oak as important species (as seed sources become available). On occasionally flooded sites a more complex forest consisting of oaks, sweetgum (*Liquidambar styraciflua*), red bay (*Persea borbonia*), holly (*Ilex opaca*), black cherry, and red maple (*Acer rubrum*) may become established. On more hydric sites, black willow (*Salix nigra*), swamp poplar (*Populus heterophylla*), and red maple can become important. Given conditions conducive to progressive succession, this latter community can be derived from a marsh elder-groundsel tree-bayberry seral stage. On the other hand, it could progress to the mesic forest type or retrogress to the more xeric, maritime forest community, depending upon seed sources and the balance between degrading erosional processes and accretional ones (Levy, 1983).

CONCLUSIONS

Previous studies and personal observations from the outer banks of North Carolina, coastal and Chesapeake Bay sites in Virginia Beach, as well as direct observations in the Virginia barrier island system tend to support the validity of the successional patterns proposed above. These successional patterns must be categorized as tentative, however, as a great deal of on-site quantification is still lacking. North Carolina patterns, although instructive, may not be transferred without hazard. The diversity of successional patterns detected throughout the coastal barrier islands tends to support concepts of Drury and Nisbet (1973) and Horn (1976) who have rather recently added fuel to the "nature of succession controversy" that has continued throughout most of this century. The Virginia barrier islands would appear to be an ideal site for studies which might help to clarify this fundamental dispute.

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Forest Vegetation Structure on the Eastern Shore of Virginia *circa* 18,000 Years B.P.

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ABSTRACT

Pollen records from 18,000 years B.P. indicate that the forests of southeastern United States were composed primarily of pine and spruce species, with lesser amounts of fir and birch. We used a simulation model of extant boreal forest dynamics to reconstruct the composition and structure of these forests on the Eastern Shore of Virginia, where full-glacial pollen was available to test the model and climate and soils data were available to drive the model. The species dominating the simulated forests were not consistent with the pollen record. In particular, the dominant pine species was white pine, yet white pine pollen has not been found in the pollen record. Although the discrepancies between simulated forests and paleoecological data indicated that our climate parameters may have been too warm, our air temperatures were consistent with appropriate reconstructions from modern analogues and atmospheric general circulation models, when corrected for possible errors. Deficiencies in the simulated effects of air temperature sums on tree growth may have caused the lack of correspondence between simulated and observed data.

Key words: forest simulation model, Delmarva peninsula, full- glacial forests

INTRODUCTION

During the last glacial maximum 22,000-13,500 years B.P., pollen assemblages throughout southeastern United States were dominated by pine (*Pinus*) and spruce (*Picea*), with some fir (*Abies*), birch (*Betula*), and minor oak (*Quercus*) pollen (Delmarva Peninsula [Sirkin *et al.*, 1977; Denny *et al.*, 1979]; Chesapeake Bay Opening [Harrison *et al.*, 1965]; Rockyhock Bay, N.C. [Whitehead, 1973, 1981]; Singletary Lake, N.C. [Frey, 1951, 1953; Whitehead, 1964]; White Pond, S.C. [Watts, 1980a,b]; Hack Pond, Va. [Craig, 1969]; Northwest Georgia [Watts, 1970]). This pine- spruce pollen zone has been interpreted as reflecting widespread jack pine (*Pinus banksiana*) and/or red pine (*Pinus resinosa*) and black spruce (*Picea mariana*) and/or red spruce (*Picea rubens*) forest vegetation throughout southeastern United States (Whitehead, 1973, 1981; Watts, 1980a,b; Delcourt and Delcourt, 1987). However, the exact structure and composition of these forests is largely unknown.

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Limitations in the floristic resolution of pollen records and difficulties in translating pollen abundance into stand structure have precluded detailed forest reconstructions. In this paper, we use a "gap" model of environmental processes and stand dynamics for boreal forests (Bonan, 1988a,b) to simulate the structure and composition of full-glacial forest vegetation in southeastern United States. We focus on the Eastern Shore of Virginia, where paleoecological data are available to test the model and climate and soils data are available to drive the model.

METHODS

Gap models of forest dynamics provide a useful means to synthesize forest ecological hypotheses (Shugart, 1984) and can be used to examine the processes controlling paleoecological forest vegetation patterns (Solomon *et al.*, 1980, 1981; Solomon and Shugart, 1984; Solomon and Webb, 1985). The boreal forest gap model (Bonan, 1988a,b) simulates the annual birth, growth, and death of individual trees on a small forest plot. Optimal tree growth is a function of a species-specific growth rate, tree diameter, and tree height and is decreased multiplicatively to the extent that site conditions (growing season temperature sums, available light, soil moisture, nutrient availability, depth of seasonal soil thawing) are less than optimal for a particular species or individual. Regeneration is constrained for these same site conditions and for other effects such as a thick forest floor organic layer, seed availability following forest fires, and vegetative reproduction. Mortality is a function of potential longevity, stress, and forest fires. Simulated fire intensity is a function of fuel buildup; fire severity is a function of forest floor moisture content.

This model simulates local and regional patterns of solar radiation, soil moisture, and soil freezing and thawing throughout northern North America, Scandinavia, and the Soviet Union (Bonan, 1988a) and forest structure and vegetation patterns in several bioclimatic regions of the North American boreal forest (Bonan, 1988a,b). Bonan (1988a,b) provides a more detailed description of model formulation. In contrast to these previous analyses, here we assumed that trees were stressed when their realized growth was less than 10% of their optimal growth.

The available species pool was limited to the major northern hardwood and boreal species of the genera (pine, spruce, fir, birch, oak) found in the pollen record (Tables 1, 2). Required parameters for these species were taken from known silvics (Fowells, 1965) or other gap model analyses (Solomon *et al.*, 1984; Bonan, 1988a,b).

Paleoecological forest reconstructions require climate data contemporary with the pollen data. Full-glacial climate conditions in southeastern United States have been estimated from the modern analogues of the pollen data (Watts, 1970, 1980a,b; Whitehead, 1981) and from atmospheric general circulation models (Manabe and Broccoli, 1985; Kutzbach and Wright, 1985; Kutzbach and Guetter, 1986; Kutzbach, 1987). As an alternative, we used data from Moran (1972) to estimate required full-glacial climate parameters (Table 3). We reconstructed mean monthly air temperatures by fitting a sine wave to Moran's (1972) mean monthly January and July air temperatures. Monthly precipitation and mean monthly cloudiness were estimated from modern values corrected for full-glacial changes in tropical storm frequency and zonal wind flow (Moran, 1972). Required long-term monthly standard deviations were obtained from climatic records from eastern Canada (Bradley *et al.*, 1985). We recognize the limitations of this approach. However, all climatic

TABLE 1. Description of required species parameters.

| | | |
|--------|---|---|
| AGEMAX | - | maximum age of species (yrs) |
| DBHMAX | - | maximum diameter at breast height (cm) |
| HTMAX | - | maximum height (m) |
| G | - | growth parameter |
| LITE | - | shade tolerance classification (1: tolerant, 2: intermediate, 3: intolerant) |
| SMOIST | - | maximum percentage of growing season that the species can tolerate soil moisture below the wilting point |
| N | - | average stump sprouts per tree |
| DMN | - | minimum diameter at breast height for sprouting (cm) |
| DMX | - | maximum diameter at breast height for sprouting (cm) |
| KTOL | - | fire tolerance (1: tolerant, 2: intermediate, 3: intolerant) |
| NUTR | - | nutrientstresstoleranceclass(1:tolerant, 2: intermediate, 3: intolerant) |
| IPFR | - | ability to grow on permafrost (1: good, 2: poor) |
| IMO | - | ability to reproduce on moss-organic layer (1: tolerant, 2: intermediate, 3: intolerant) |
| IBW | - | vulnerability to spruce budworm outbreaks (1: high, 2: low) |
| ALC | - | fraction of full sunlight when reproduction is inhibited |
| GDDMIN | - | minimum growing degree-days in the species' range |
| GDDMAX | - | maximum growing degree-days in the species' range |
| SWTCH | - | reproduction switches [SWTCH(1) is true if the species has serotinous cones. SWTCH(2) is true if the species has copious, light, wind dispersed seeds. SWTCH(3) is true if the species can reproduce by layering]. |

reconstructions incorporate errors to various degrees. Comparisons of our climate estimates with previous estimates provides an additional test of the validity of our forest reconstruction independent of the comparisons of simulated and observed vegetation data.

Pollen data typically record vegetation at the scale of 100- 1,000 km² (Delcourt and Delcourt, 1987). By averaging forest dynamics over many plots, gap models simulate forest vegetation over a similar spatial area (Solomon and Webb, 1985). However, this area is assumed to be homogenous in terms of climate and soil parameters. Although separate simulations can characterize forest dynamics for different site conditions, interfacing gap models with pollen data requires reconstruction of forests over the composite of habitats that the palynological data record.

Full-glacial forest habitats on the Delmarva peninsula are thought to range from freshwater bogs and swamps to extensive sand barrens (Emery *et al.*, 1967; Denny and Owens, 1979; Denny *et al.*, 1979). In these analyses, we used three different site conditions: mesic, nutrient rich; mesic, nutrient poor; and dry sites (Table 4). In addition, fire is an important component of modern boreal forests (Bonan, 1988a). Each site condition was replicated under short and long fire cycles.

Table 2. Species parameters. Dashes indicate extraneous parameters.

| | AGE MAX | DBH MAX | HT MAX | G | LITE | SMOIST | N | DMN | DMX | KTOL | NUTR | IPFR | IMO | IBW | ALC | GDD MIN | GDD MAX | SWITCH |
|--|------------|------------|-----------|-------|------|--------|---|-----|-----|------|------|------|-----|-----|-----|------------|------------|--------|
| <i>Abies balsamea</i> Balsam fir | 200 | 86 | 23 | 103.1 | 1 | 0.20 | - | - | - | 3 | 1 | 2 | 1 | 1 | - | 560 | 2386 | FFT |
| <i>Betula alleghaniensis</i> Yellow birch | 300 | 100 | 31 | 90.8 | 2 | 0.20 | 3 | 12 | 50 | 3 | 2 | - | 2 | - | 0.6 | 1100 | 2700 | FTF |
| <i>Betula papyrifera</i> White birch | 140 | 76 | 30 | 187.2 | 3 | 0.30 | 1 | 10 | 32 | 3 | 1 | 2 | 2 | - | 0.6 | 484 | 2036 | FTF |
| <i>Picea glauca</i> White spruce | 200 | 76 | 34 | 147.3 | 1 | 0.30 | - | - | - | 3 | 1 | 2 | 2 | 2 | - | 280 | 1911 | FFF |
| <i>Picea mariana</i> Black spruce | 250 | 46 | 27 | 93.5 | 1 | 0.30 | - | - | - | 3 | 1 | 1 | 1 | 2 | - | 247 | 1911 | TFT |
| <i>Picea rubens</i> Red spruce | 400 | 60 | 23 | 50.9 | 1 | 0.30 | - | - | - | 3 | 1 | - | 2 | 2 | - | 1247 | 2462 | FFF |
| <i>Pinus banksiana</i> Jack pine | 150 | 64 | 30 | 173.8 | 3 | 0.50 | - | - | - | 1 | 1 | 2 | 3 | - | 0.3 | 830 | 2216 | TFF |
| <i>Pinus resinosa</i> Red pine | 300 | 91 | 30 | 87.8 | 3 | 0.40 | - | - | - | 1 | 1 | - | 3 | - | 0.3 | 1100 | 2035 | FFF |
| <i>Pinus strobus</i> Eastern white pine | 450 | 102 | 46 | 87.6 | 2 | 0.30 | - | - | - | 2 | 1 | - | 2 | - | 0.2 | 1100 | 3165 | FFF |
| <i>Quercus rubra</i> Northern red oak | 400 | 100 | 30 | 66.0 | 2 | 0.30 | 2 | 12 | 40 | 3 | 2 | - | 3 | - | - | 1100 | 4571 | FFF |

TABLE 3. Modern and full-glacial climatic parameters.

| Month | Temperature ^a | | | Precipitation ^a | | | Cloudiness ^b | |
|-------|--------------------------|--------|-----------|----------------------------|--------|-----------|-------------------------|--------|
| | 18,000 B.P. | Modern | Std. Dev. | 18,000 B.P. | Modern | Std. Dev. | 18,000 B.P. | Modern |
| J | 2.6 °C | 3.8 °C | 2.1 | 8.0 cm | 8.4 cm | 2.9 | 0.4 | 0.6 |
| F | 4.0 | 4.5 | 2.3 | 8.0 | 8.3 | 3.1 | 0.4 | 0.6 |
| M | 6.6 | 8.1 | 1.9 | 10.0 | 10.2 | 3.9 | 0.5 | 0.5 |
| A | 10.0 | 13.4 | 1.3 | 7.0 | 7.5 | 2.9 | 0.5 | 0.7 |
| M | 14.2 | 18.5 | 1.2 | 8.0 | 8.2 | 3.6 | 0.5 | 0.5 |
| J | 16.2 | 22.9 | 1.2 | 8.5 | 9.1 | 3.9 | 0.6 | 0.6 |
| J | 17.0 | 25.2 | 1.3 | 9.5 | 11.4 | 4.4 | 0.6 | 0.5 |
| A | 16.2 | 24.3 | 1.3 | 8.5 | 11.4 | 4.3 | 0.6 | 0.6 |
| S | 14.2 | 21.2 | 1.3 | 8.0 | 8.8 | 4.1 | 0.5 | 0.6 |
| O | 10.0 | 15.8 | 1.2 | 7.5 | 8.6 | 3.4 | 0.5 | 0.3 |
| N | 6.6 | 10.3 | 1.6 | 7.0 | 7.8 | 2.8 | 0.5 | 0.5 |
| D | 4.0 | 4.8 | 1.9 | 7.5 | 8.3 | 3.0 | 0.4 | 0.6 |

July average minimum temperature: 8°C (18,000 B.P.), 20°C (modern)

July average maximum temperature: 25°C (18,000 B.P.), 30°C (modern)

Latitude: 37.6°

Longitude: 75.8°

Elevation: 5 m

Slope: 0 %

^a modern value from Painter, Va (Crockett, 1972)

^b modern value from Norfolk, Va (NOAA, 1987)

TABLE 4. Full-glacial site parameters used in the simulation model.

| SITE | MOISTURE CONTENT ^a | | | Relative Nutrient Availability | FIRE REGIME | |
|-------------------------|-------------------------------|----|-----|--------------------------------------|--------------------|------------------------|
| | SAT | FC | PWP | | Cycle ^b | Intensity ^c |
| mesic, nutrient rich | 35 | 25 | 10 | 1.00 200 | 100 10 | 10 |
| mesic, nutrient poor | 35 | 25 | 10 | 0.33 200 | 100 10 | 10 |
| dry | 18 | 12 | 5 | 1.00 | 0 100 | 10 10 |

^a soil moisture contents at saturation SAT, field capacity FC, and permanent wilting point PWP (cm)

^b inverse of the annual probability of a stand burning (yrs)

^c stand biomass at which fires are catastrophic (kg/m²)

The fire intensity parameter was set to ensure the majority of fires were catastrophic. These parameters mimicked the fire regime of modern northern forests (Bonan, 1988a).

RESULTS

Reconstructed air temperatures showed decreased seasonality in which summers were colder than prevailing conditions, but winters were not much different from modern conditions (Table 3). Simulated full-glacial solar radiation was not much different from modern values (Fig. 1). Orbital parameters at both times are similar (Berger, 1978) and the only simulated differences were due to slight changes in estimated full-glacial cloud cover. Air temperature and solar radiation were used to estimate potential evapotranspiration (Bonan, 1988a,b). Simulated potential evapotranspiration was reduced under the colder climate 18,000 years B.P. (Fig. 2), offsetting the lower summer precipitation (Table 3) so that the monthly water deficit decreased from modern values.

For each of the six different site and fire cycle combinations, forest composition was determined based on relative species biomass after 500 years of simulation, when forest composition and structure approximated equilibrium conditions (Shugart, 1984). On all sites, pine was the dominant taxon (Table 5). White pine was the dominant species; jack pine was of secondary importance. Balsam fir, red spruce, and yellow birch were also important. White spruce, black spruce, and white birch did not grow on any of the six site conditions. Red pine and red oak were minor components of the simulated forest.

DISCUSSION

Gap models simulate tree biomass whereas palynological data record relative pollen abundance. Taxon calibrations have been developed to translate the observed pollen spectrum into the composition of surrounding forest vegetation (*e.g.*, Webb *et al.*, 1981; Delcourt *et al.*, 1984). At the generic level the simulated forest structure and composition closely matched Delcourt and Delcourt's (1987) forest reconstruction for the Delmarva Peninsula (Table 6). However, using taxon calibrations to estimate forest structure is fraught with difficulties and interpretations of pollen-based forest structure must be made with caution (Webb *et al.*, 1981; Solomon, 1986b; Prentice and Webb, 1986; Prentice, 1988).

Regardless of this problem, the species-level composition of the simulated forests was not consistent with fossil pollen analyses. All simulated forests were dominated by white pine (Table 5). However, the pollen of white pine, a *Haploxylon* pine species which from pollen morphology can be distinguished from *Diploxylon* pine species (Whitehead, 1964; Craig, 1969; Watts, 1979), has not been found during full-glacial conditions on the coastal plain of northeastern North Carolina (Whitehead, 1981). Indeed, the full-glacial, southeastern United States pine-spruce zone is thought to indicate jack pine (*Pinus banksiana*) and/or red pine (*Pinus resinosa*) and black spruce (*Picea mariana*) and/or red spruce (*Picea rubens*) forest vegetation (Whitehead, 1973, 1981; Watts, 1980a,b; Delcourt and Delcourt, 1987). Moreover, fossilized full-glacial white spruce cones have been identified in the coastal plain of Georgia (Watts, 1980a), yet white spruce could not grow under our reconstructed climate for the Eastern Shore.

EASTERN SHORE, VIRGINIA

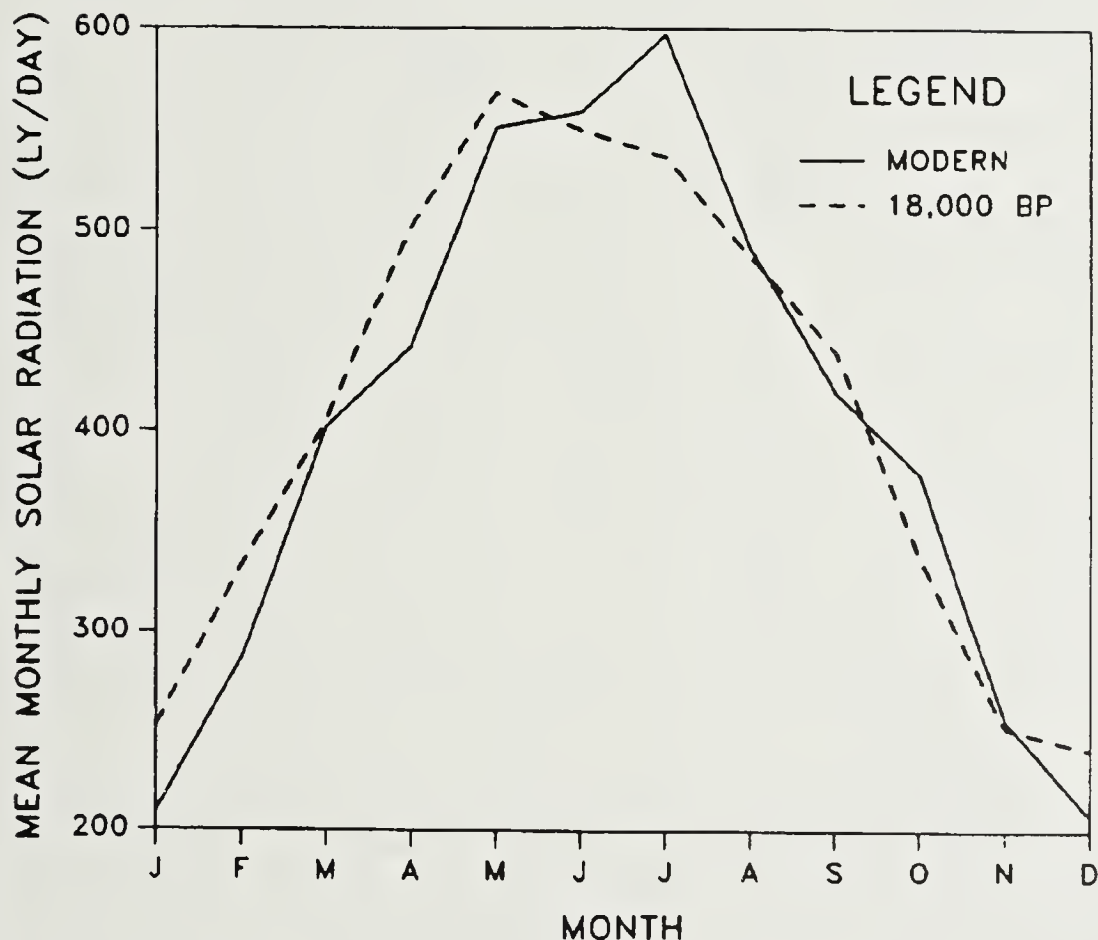


FIGURE 1. Simulated mean monthly solar radiation: modern and 18,00 years B. P.

Some researchers have speculated that white pine found full-glacial refugia in the west (Craig, 1969; Watts, 1970). Forest dynamics were simulated again, but this time without white pine in the species pool (*i.e.*, assuming that white pine had refugia further west). Again simulated species composition was inconsistent with paleoecological data. In particular, on the dry site, which is thought to have been extensive throughout the Delmarva Peninsula during full-glacial conditions (Denny and Owens, 1979; Denny *et al.*, 1979), jack pine contained up to 50% of stand biomass, and spruce, birch, and fir were of less importance (Table 7). However, red oak comprised 9% of stand biomass. There is some controversy whether the oak pollen found in this region is significantly above background levels (Delcourt and Delcourt, 1987; Webb, 1987, 1988). Oak is a prolific producer of pollen and the low relative pollen abundance (0-5% arboreal pollen [Harrison *et al.*, 1965; Sirkin *et al.*, 1977]) does not indicate the amount of oak simulated in these analyses.

The discrepancies between simulated forests and paleoecological data could have reflected climatic parameters that were warmer than the actual climate 18,000 years B.P. Available growing degree-days (5.6°C base) for our reconstructed climate averaged 1865 degree-days and with stochastic variation ranged from 1567-2336. This range exceeded the maximum growing degree-days for white birch, white spruce, black spruce, jack pine, and red pine. Only balsam fir, yellow birch,

EASTERN SHORE, VIRGINIA

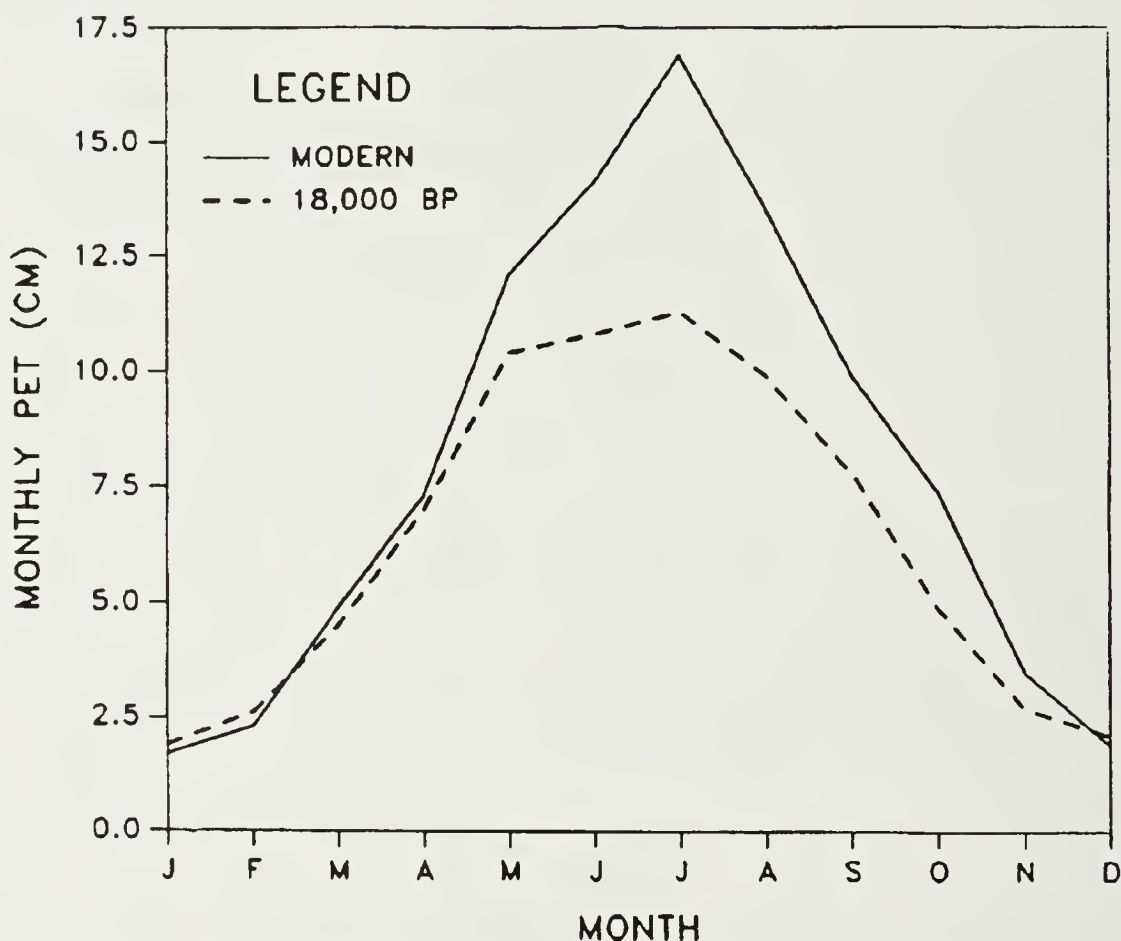


FIGURE 2. Simulated monthly potential evapotranspiration (PET): modern and 18,00 years B. P.

white pine, and northern red oak had growing degree-day parameters within the simulated range (Table 2).

The climate parameters used in these analyses were not much different than those reconstructed from pollen analyses. Our mean July temperature (17.0°C) was similar to pollen-derived estimates for southeastern United States (16 to 20°C [Watts, 1970, 1980a,b; Whitehead, 1981]). We used a warmer mean January temperature (2.6°C) than pollen-derived reconstructions (-10 to -22°C [Watts, 1970, 1980a,b; Whitehead, 1981]). However, these modern analogue estimates did not incorporate important full-glacial changes in seasonality. Our reconstructed air temperatures were consistent with Bryson and Wendland's (1967) and Solomon and Shugart's (1984) hypothesis of decreased seasonality during full-glacial conditions in which summers were colder than present but winters were not much different than present. Full-glacial climates simulated by atmospheric general circulation models indicated similar conditions (Manabe and Broccoli, 1985; Kutzbach and Wright, 1985; Kutzbach and Guetter, 1986; Kutzbach, 1987).

Results from the National Center for Atmospheric Research Community Climate Model (NCAR CCM) atmospheric general circulation model indicated full-glacial mean January and July temperatures were decreased by 0 - 5°C from modern values throughout southeastern United States (Kutzbach and Wright,

TABLE 5. Simulated forest structure for the six different forest sites.

| | NUTRIENT RICH | | NUTRIENT POOR | | DRY SITE | |
|--------------|---------------|---------|---------------|---------|------------|---------|
| | Fire Cycle | | Fire Cycle | | Fire Cycle | |
| | 100 yrs | 200 yrs | 100 yrs | 200 yrs | 50 yrs | 100 yrs |
| Balsam fir | 11.6 % | 10.8 % | 19.7 % | 17.9 % | 10.5 % | 12.3 % |
| Birch spp. | 19.8 | 14.1 | 10.7 | 5.4 | 23.7 | 20.6 |
| Yellow birch | 19.8 | 14.1 | 10.6 | 5.4 | 23.0 | 20.4 |
| White birch | 0.0 | 0.0 | 0.1 | 0.0 | 0.7 | 0.2 |
| Red spruce | 11.3 | 20.3 | 10.2 | 19.5 | 5.2 | 8.2 |
| Red oak | 0.9 | 0.3 | 0.7 | 0.5 | 3.1 | 0.9 |
| Pine spp. | 56.5 | 54.4 | 58.6 | 56.5 | 57.5 | 57.9 |
| Jack pine | 20.4 | 8.5 | 17.6 | 7.9 | 35.3 | 20.5 |
| Red pine | 0.2 | 0.1 | 0.4 | 0.2 | 1.4 | 0.6 |
| White pine | 35.9 | 45.8 | 40.6 | 48.4 | 20.8 | 36.8 |

1985; Kutzbach and Guetter, 1986; Kutzbach, 1987). Applying this range of temperature reductions to modern temperatures on the Eastern Shore results in a January temperature (-1 to 4°C) similar to ours but a warmer July temperature (20 to 25°C). Manabe and Broccoli (1985) used a different atmospheric general circulation model coupled with an oceanic model to simulate full-glacial climate conditions. They also found that winter and summer surface temperatures in southeastern United States were only 0- 4°C colder than modern values.

However, summer air temperatures simulated by general circulation models may be too warm. Webb *et al.* (1987) coupled modern pollen/climate response surfaces and climate data generated by the NCAR CCM to reconstruct pollen spectra for the past 18,000 years. During full-glacial conditions, these simulations underestimated spruce and northern pine pollen and overestimated oak pollen in southeastern United States. These errors may indicate the simulated climate was too warm by 2-4°C (Webb *et al.*, 1987). Applying this reduction to the NCAR CCM July temperature estimate results in temperatures ranging from 16 to 23°C, which is more consistent with our value.

Our annual precipitation (98 cm) was also consistent with the range of estimated values. Modern analogue estimates of annual precipitation in southeastern United States range from drier than normal (70-75 cm [Watts, 1970; Whitehead, 1981]) to slightly drier than normal (105 cm [Watts, 1980a,b]). NCAR CCM simulations indicate winter precipitation was unchanged and summer precipitation was decreased by 25-30% of modern values (Kutzbach and Wright, 1985; Kutzbach and Guetter, 1986; Kutzbach, 1987). Applying a 30% reduction to modern growing season (May to September) precipitation on the Eastern Shore results in an annual precipitation of 93 cm. Manabe and Broccoli (1985) found that annual precipitation in the region of the Eastern Shore was reduced by 0.0-0.05 cm/day from modern

TABLE 6. Observed and simulated full-glacial forest structure.

| Genera | Observed ^a | Simulated |
|--------|-----------------------|-----------|
| Pine | 50 % | 54-59 % |
| Spruce | 15-35 | 5-20 |
| Fir | 10 | 10-20 |
| Birch | 12 | 5-24 |
| Oak | minor | 0-3 |

^a from Delcourt and Delcourt (1987)

TABLE 7. Simulated forest structure: without white pine.

| | NUTRIENT RICH | | NUTRIENT POOR | | DRY SITE | |
|--------------|---------------|---------|---------------|---------|------------|---------|
| | Fire Cycle | | Fire Cycle | | Fire Cycle | |
| | 100 yrs | 200 yrs | 100 yrs | 200 yrs | 50 yrs | 100 yrs |
| Balsam fir | 20.9 % | 23.3 % | 36.4 % | 0.7 % | 8.7 % | 24.5 % |
| Birch spp. | 42.5 | 36.2 | 20.7 | 20.9 | 17.9 | 24.1 |
| Yellow birch | 42.3 | 36.0 | 20.6 | 20.9 | 17.8 | 23.9 |
| White birch | 0.2 | 0.2 | 0.1 | 0.0 | 0.1 | 0.2 |
| Red spruce | 13.1 | 24.0 | 21.9 | 35.0 | 12.9 | 12.3 |
| Red oak | 1.1 | 0.9 | 1.5 | 1.7 | 9.4 | 5.5 |
| Pine spp. | 22.4 | 15.5 | 19.6 | 11.7 | 51.1 | 33.6 |
| Jack pine | 21.9 | 15.2 | 19.1 | 11.5 | 50.5 | 32.8 |
| Red pine | 0.5 | 0.3 | 0.5 | 0.2 | 0.6 | 0.8 |

values. Applying this reduction to modern values results in annual precipitation of 90 to 108 cm.

In short, the full-glacial climate parameters we used in our analyses were consistent with the range of appropriate previous estimates. The discrepancies between observed paleoecological data and simulated forests may, therefore, have reflected inadequacies in the forest simulation model. Of particular importance in the context of paleoecological forest reconstructions is the growing degree-days growth multiplier, which is used to scale tree growth and regeneration for sub-optimal air temperatures. The effect of air temperature sums on individual tree performance is assumed to be parabolic, scaled to zero at the minimum and maximum growing degree-days in a species' range and scaled to one halfway between these values (Shugart, 1984). This formulation causes tree growth and

reproduction to decline to zero as climatic conditions approach the northern and southern range limits of a species.

In these analyses, we used Solomon *et al.*'s (1984) growing degree-day parameters (Table 2). In geographic testing of a gap model, this parameterization of climate/vegetation interactions resulted in simulated regional forest vegetation patterns that were consistent with observed patterns (Solomon *et al.*, 1984; Solomon, 1986a). However, our analyses indicate that these parameters may be wrong. Moreover, the formulation of the growing degree-day growth multiplier may have accentuated differences between observed and simulated forest composition. The parabolic form of the growth multiplier causes the model to be quite sensitive to slight differences in annual growing degree-days when at the edges of a species' range and insensitive when in the center of its range. Solomon *et al.*'s (1984) parameters put our reconstructed climate at or near the southern range limit of many of the simulated tree species. Clearly, the validity of the parabolic growth multiplier must be resolved before gap models can provide robust projections of the ecological consequences of climate changes.

This study has highlighted the importance of interfacing forest stand models with paleoecological data. An accurate understanding of paleoclimates and paleoecological forest composition can only occur through independent forest and climate reconstructions. Forest stand models provide one means of doing so. In addition, paleoecological data provide a controlled test of these models and can help to identify inaccuracies in model formulation (e.g., air temperature effects). Such testing is necessary given the widespread use of gap models to project the ecological consequences of future climate change scenarios (e.g., Solomon *et al.*, 1984; Solomon, 1986a; Pastor and Post, 1988).

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Small Mammal Population Densities and Habitat Associations on Chincoteague National Wildlife Refuge, Assateague Island, Virginia

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ABSTRACT

Evaluation of small mammal distributions in Chincoteague National Wildlife Refuge show that each species exhibited specific habitat associations. *Microtus pennsylvanicus* was the most numerous followed by *Oryzomys palustris*, *Mus musculus*, *Cryptotis parva*, and *Peromyscus leucopus*. *Microtus* showed the lowest variation in population density while the remaining four species showed clear seasonal shifts in density. *Peromyscus* were not associated with any of the other species and occurred primarily in the pine wood habitats. The other four species occurred in both the dune and marsh habitats. *Microtus* tended to occupy microhabitats in which monocot vegetation and abundant ground cover occurred, *Oryzomys* were most common in moist microhabitats and were locally abundant in tidal creek areas. *Mus* were abundant in the open habitat of the dune grassland, but also occurred in shrub dominated habitats. *Cryptotis* were common at relatively open sites in the shrub-marsh edge habitat as well as in open microhabitats of the dune grassland area. *Microtus* were reproductively active in every month except January, while the other species exhibited seasonal reproductive patterns.

Key words: Population density, habitat associations, *Microtus*, *Mus*, *Cryptotis*, *Peromyscus*, *Oryzomys*.

INTRODUCTION

Habitat associations and population density estimates of small mammals on the Virginia barrier islands are frequently limited to data gathered from line transects or from rather short-term studies (Paradiso and Handley, 1965; Dueser and Brown, 1980; Porter and Dueser, 1982). For the most part, these studies have reported on species occurrence, habitat associations, and have speculated on the importance of competition in determining/influencing community structure. Adkins (1980) concluded, from a year-round study on Assateague, that habitat separation among five of six common small mammal species was minimal and that

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interspecific competition was pervasive among species sharing habitats. Direct evidence for competition was lacking in a reciprocal removal experiment as no habitat shift or density change occurred (Scott, 1983). Evidence for strong interspecific competition also was not reported by Dueser and Porter (1986) and habitat selection seemed to be the more important variable in sorting the species assemblage on Assateague island.

This research examines population densities over seasons, years, and habitat associations among the common small mammal species on Assateague Island. Evaluation of a number of habitat variables permitted examination of niche overlap over the course of the study period. These data were then compared to results previously reported which permitted an evaluation of the importance of habitat selection by species within this community.

METHODS

The study sites were located within the Chincoteague National Wildlife Refuge, Assateague Island, Virginia. Three non-adjacent trapping grids were established in June 1983 and were trapped bi-monthly until March 1985 when two of the grids were destroyed by fire. The grids were located in dune grassland, marsh, and pine woodland habitats which incorporated the major habitat types available on the island (Higgins *et al.*, 1971; Hill, 1986). Grids (0.64 ha) were permanently staked to ensure that the same sites were used in subsequent trapping sessions. Each trap grid was well within a habitat type with the nearest habitat edge more than 20 m beyond a grid boundary. Traps were set at 10 m intervals on 9 by 9 square arrays with two traps per station. Capture data from both trap stations were used in all subsequent analysis except as otherwise noted. One small (165x64x51 mm) and one large (279x89x76 mm) Sherman trap was placed at each station and was baited with crimped oats. During winter, traps were provisioned with supplemental food and cotton nest material to improve survival. Traps were checked twice daily for five days during each trapping period. All small mammals were toe-clipped upon first capture for individual identification. On each capture, body mass, total length and reproductive condition (position and size of testis, perforate or non-perforate vagina, teat condition, and presence of palpable embryos) were recorded.

Each grid was characterized, based on frequency of occurrence, by particular vegetation types. On the woods grid, *Pinus taeda* formed the overstory canopy while the understory was composed of *Panicum virgatum*, *Spartina alterniflora*, *Hydrocotyle verticillata*, *Parthenocissus quinquefolia*, *Iva frutescens*, *Myrica cerifera* and *Rhus radicans*. The marsh and dune grids lacked any significant overstory canopy. The marsh was dominated by *Distichlis spicata* and *Spartina patens* with *Myrica cerifera*, *Baccharis halimifolia* and *Iva frutescens* also present. *Juncus dichotomus*, *Panicum scoparium*, *Scirpus americana* and *Spartina patens* formed the greatest proportion of the monocots on the dune grid. In addition, *Solidago sempervirens*, *Lepidium virginicum* and *Eupatorium pubescens* were common forbs, while *Myrica cerifera* and *M. pennsylvanica* formed the dune grid shrub layer. The great variety of plant species on the dune grid produced a wider variety of microhabitats. This was the only location where all seven species of small mammals were captured.

TABLE 1. Habitat variables used to calculate multivariate microhabitat overlap and their method of measurement.

| Variable | Description |
|----------|---|
| Gras cov | Percent cover of grasses and sedges within a 1.0 m ² quadrat centered on the trap station |
| Forb cov | Same as grass except forbs only |
| Shrb cov | Same as grass except shrubs only |
| Wood cov | Same as grass except woody species only |
| Shrb sps | Number of shrub species within a 5.0 m radius circle centered on the trap station |
| Litter | Mean depth (cm) of litter layer determined from 4 measurements taken within a 1.0 m ² quadrat centered on the trap station |
| Htveg | Height of tallest vegetation (excluding canopy trees) within a 5.0 m radius circle centered on the trap station |
| Flood | Depth (cm) of spring tide flooding |

Each trap site was characterized with a series of quantitative microhabitat variables (Dueser and Shugart, 1978; Geier and Best, 1980; Kitchings and Levy, 1981). Sixteen habitat variables were measured during the summer trapping period, 8 of which were used in the habitat analysis: percent cover of grass (Gras cov), forbs (Forb cov), shrubs (Shrb cov) and woody species (Wood cov), height of understory vegetation (Htveg), shrub species (Shrb spp), litter depth (Litter), and height of the spring flood (Flood) (Table 1). Discriminant function analysis was then used to determine if small mammal species differed with respect to habitat variables (SAS Candisc procedure; SAS Institute, 1982). The number of sample groups (*i.e.*, species) in these analyses was six in summer samples (June - September) and five in all others. Only data from the first capture of an individual during a trap session were used in the analyses. Habitat variables associated with the capture of mammal species were analyzed using canonical variate analysis (SAS Candisc procedure; SAS Institute, 1982). The multivariate niche overlap measure of MacArthur and Levins (1967) was used to evaluate niche overlap among the five abundant species. The overlap was estimated from habitat utilization data from trapping records using discriminant function analyses (Harner and Whitmore, 1977). Population densities were calculated by minimum number alive method (Krebs, 1966).

RESULTS

There were 2430 trap nights per trap session and a total of 24,300 trap nights which resulted in 3856 captures over the study period. The relative efficiency of large and small traps in capturing small mammals did not differ significantly among different trapping periods ($X^2 = 4.15$, $P > 0.20$), but species which have large body size were more frequently captured in large traps (Maly and Cranford, 1985). A total of 567 individuals were captured of the five common species: *Mus musculus* (128), *Microtus pennsylvanicus* (167), *Oryzomys palustris* (131), *Peromyscus*

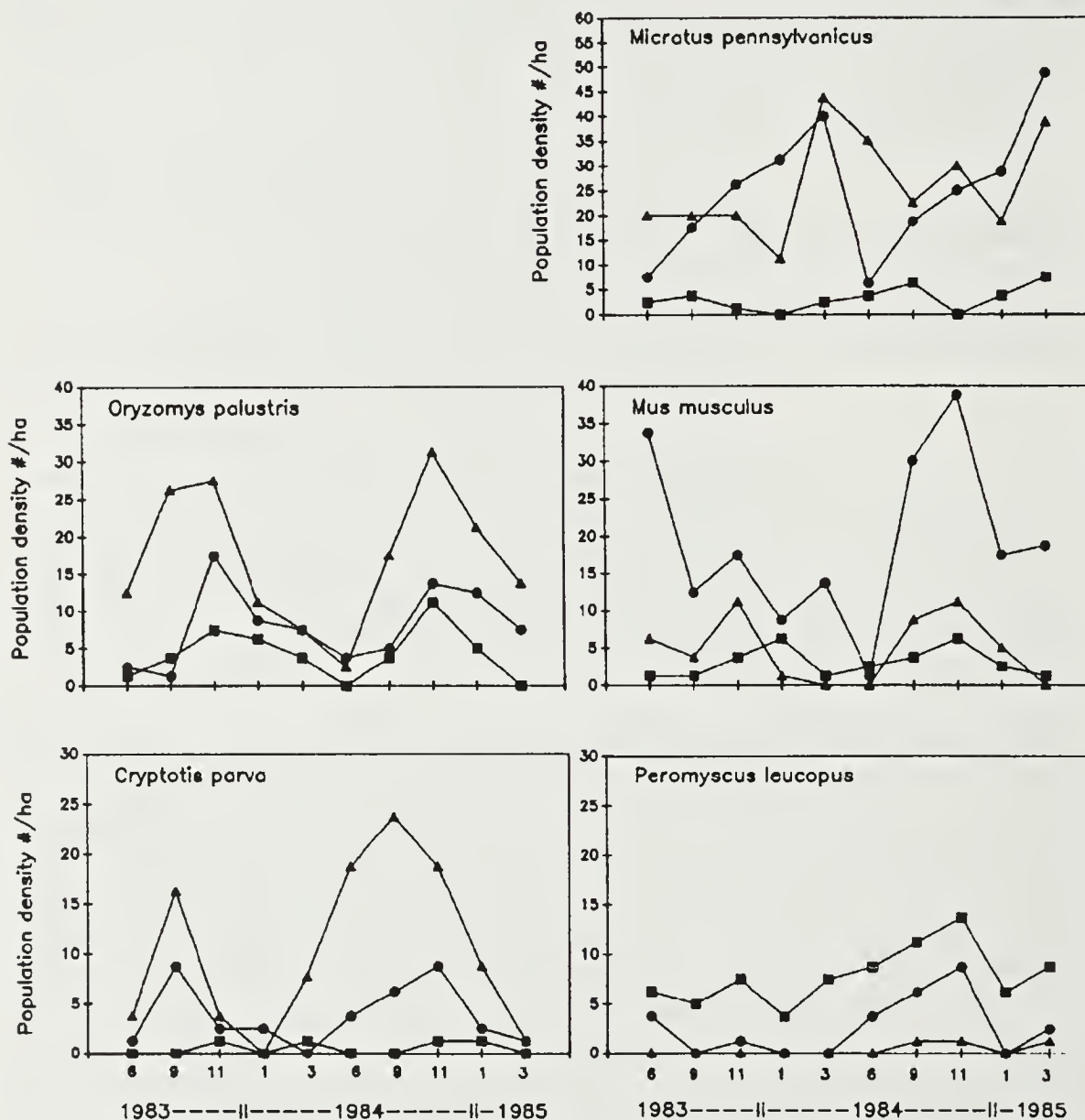


FIGURE 1. The minimum number known to be alive of the five common species on the three grids (Marsh, Dune and Pine Woods) from June 1983 to March 1985. The months are represented on the X-axis by their numerical value. Dune data plotted as circles, marsh by triangles and pine woods by squares.

leucopus (56), and *Cryptotis parva* (85). In addition, *Rattus norvegicus* (3) and *Zapus hudsonius* (26) were captured but not in sufficient numbers for further analysis. Population densities of five of the seven species (*Peromyscus leucopus*, *Mus musculus*, *Microtus pennsylvanicus*, *Oryzomys palustris*, and *Cryptotis parva*) varied both by habitat, season, and by year (Fig. 1), *Mus*, *Microtus* and *Cryptotis* rarely occurred on the woods grid, but with the exception of *Peromyscus* all these small mammal species occurred on the marsh and dune grids. *Mus* was most common on the dune grid, while *Oryzomys* and *Cryptotis* were most common on the marsh grid. *Microtus* occurred with nearly equal numbers on both the dune and marsh grids, *Mus*, *Cryptotis*, and *Oryzomys* reached highest densities in late fall and showed clear seasonal changes in densities, while *Microtus* peaked in late spring and showed smaller seasonal shifts in densities. *Peromyscus leucopus* was very rare on the marsh

TABLE 2. Discriminant function analysis of small mammal microhabitats both monthly and overall using the 8 habitat variables. The upper half of the figure reports the number of each species caught in that sample. The lower portion reports the correlation coefficient (r) of that variable with the first discriminant function.

| Variable | Jun. | Aug. | Nov. | Jan. | Mar. | Overall |
|-------------------|---------------------|-------|-------|-------|-------|---------|
| <i>Cryptotis</i> | 20 | 40 | 27 | 14 | 9 | - |
| <i>Mus</i> | 31 | 42 | 64 | 30 | 25 | - |
| <i>Microtus</i> | 52 | 59 | 69 | 60 | 96 | - |
| <i>Oryzomys</i> | 16 | 41 | 75 | 47 | 30 | - |
| <i>Peromyscus</i> | 16 | 18 | 23 | 7 | 15 | - |
| Gras cov | 0.78 | 0.84 | 0.47 | 0.06 | 0.69 | 0.70 |
| Forb cov | -0.24 | -0.10 | -0.04 | -0.29 | -0.29 | -0.08 |
| Shrb cov | -0.70 | -0.38 | -0.29 | 0.57 | 0.09 | -0.36 |
| Wood cov | -0.46 | -0.50 | 0.03 | -0.06 | -0.19 | -0.24 |
| Shrb sps | -0.35 | -0.45 | -0.04 | 0.10 | 0.19 | -0.18 |
| Litter | 0.71 | 0.59 | 0.18 | 0.02 | 0.31 | 0.30 |
| Htveg | -0.92 | -0.59 | -0.86 | -0.90 | -0.59 | -0.75 |
| Flood | 0.42 | 0.64 | 0.15 | 0.23 | 0.11 | 0.25 |
| Wilk's Lambda | 0.20 | 0.10 | 0.46 | 0.47 | 0.32 | 0.39 |
| p value | all less than 0.001 | | | | | |

grid, common on the woods grid, and only present on the dune grids in 1984 from July to November. Reproduction in *Mus* and *Oryzomys* began in May and continued through November while in *Cryptotis* it occurred from March through October. *Microtus* were reproductively active in all samples except January 1984, but the proportion of reproductively active females varied from 18% in winter to 75% in summer. *Peromyscus* was reproductively active from March through September. For all species studied, young born early in the reproductive season became reproductively active during that season. Young of *Mus* and *Oryzomys* born late in the year did not reproduce until the following spring.

The correlation coefficients between the first discriminant function for small mammal captures and the habitat variables indicate that grass cover and the height of the vegetation were most important (Table 2.). These two variables distinguished between the species based on microhabitat use. In general, grass cover was the most important variable in separating habitat occurrence except in November and January when it was not highly correlated with the first discriminant function. In that time period vegetation height, previously the second most important variable, was highly correlated along with shrub cover in January. Seasonal differences in each variable are clear and thus reflect the differential use by small mammals of the microhabitat space over time. The Wilk's lambda statistic (SAS Candisc Procedure, 1982) was significant for all sample dates as well as for the overall analysis. This clearly indicates that the small mammal species present did differ with respect to habitat use. For most sample intervals the first discriminant function

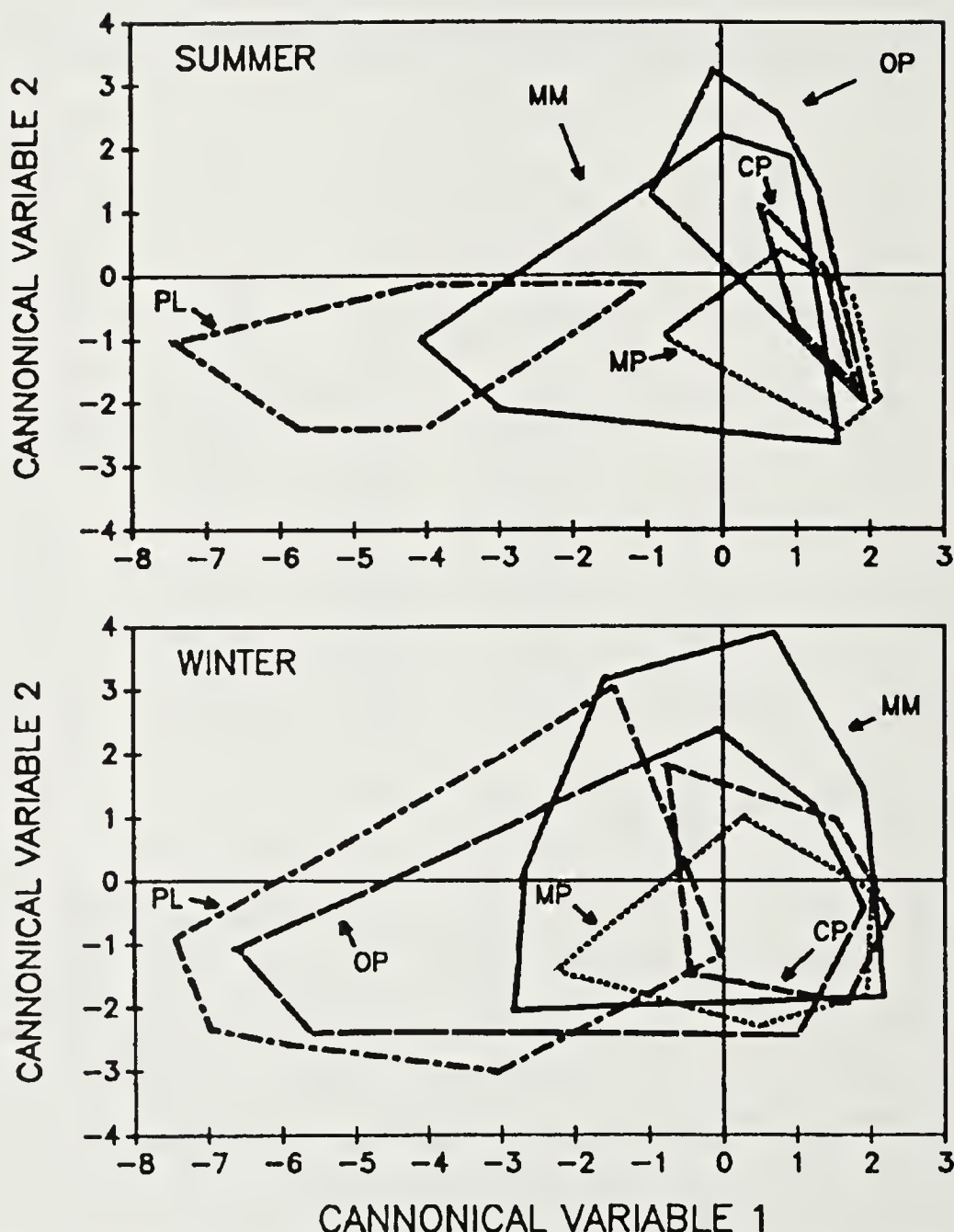


FIGURE 2. The enclosed spaces surround all the capture stations which caught a particular species. Each species is indicated by a two letter abbreviation which is the first letter of the genus name followed by the first letter of the species name. The upper panel utilized the June capture data and represents "Summer" while the lower panel is the November capture data representing "Winter".

accounted for 52-65% of the variance, while the second accounted for an additional 22-33%.

Microhabitat overlap between species pairs varied considerably with season (Table 3). For *Peromyscus* the association with woods greatly reduces the possible overlap with the other species which rarely occur in that habitat. The other three species show considerable overlap over time, especially during the winter months. Mean community overlap did not differ significantly over time. However, if *Peromyscus* was excluded, microhabitat overlap was considerably higher in winter for the other species. This shift in habitat use and hence microhabitat overlap can also be seen in the two plots of capture locations for all species with respect to the

TABLE 3. Microhabitat overlap between 5 pairs of small mammals resident on the grids,

| SpeciesMicrohabitat Overlap | | | | | | |
|-----------------------------|------|------|------|------|------|------|
| Pair | Jun. | Aug. | Nov. | Jan. | Mar. | Mean |
| Mus -Cryptomys | 0.05 | 0.10 | 0.13 | 0.19 | 0.10 | 0.11 |
| Mus -Microtus | 0.47 | 0.31 | 0.87 | 0.76 | 0.60 | 0.60 |
| Mus-Oryzomys | 0.44 | 0.58 | 0.86 | 0.87 | 0.40 | 0.63 |
| Mus-Peromyscus | 0.33 | 0.38 | 0.33 | 0.10 | 0.09 | 0.25 |
| Microtus-Cryptomys | 0.32 | 0.35 | 0.50 | 0.65 | 0.28 | 0.42 |
| Microtus-Oryzomys | 0.45 | 0.19 | 0.80 | 0.80 | 0.75 | 0.60 |
| Microtus-Peromyscus | 0.07 | 0.01 | 0.00 | 0.02 | 0.04 | 0.08 |
| Oryzomys-Cryptomys | 0.35 | 0.40 | 0.68 | 0.84 | 0.35 | 0.52 |
| Oryzomys-Peromyscus | 0.09 | 0.05 | 0.25 | 0.29 | 0.27 | 0.19 |
| Peromyscus-Cryptomys | 0.06 | 0.05 | 0.08 | 0.10 | 0.13 | 0.08 |
| Overall | 0.23 | 0.24 | 0.45 | 0.44 | 0.30 | 0.33 |

first two canonical variables (Fig. 2). Although the distribution of captures shows considerable overlap along these axes, the "winter" (November data) plot shows the increased microhabitat overlap and, in general, reflects a wider range in usage of habitat by these species (Table 3).

DISCUSSION

Population densities varied with season and exhibited similar patterns during each year of the study. *Peromyscus* was the most restricted species in distribution and the lowest in

population density. Although each species was absent at least once on a study grid, *Peromyscus* was missing from the marsh grid for the first year of the study. Our data and those reported by Kirkland and Fleming (this volume, 1988) both demonstrate that *Mus* and *Peromyscus* had little spatial overlap with the former showing a preference for dune habitat and the latter the woods habitat. *Microtus* was the most abundant and most widely distributed. Additionally, *Microtus* exhibited nearly continuous reproduction on the study areas while the other species had clear seasons in which no reproductively-active individuals were noted.

Habitat affinities of mammals in the present study were similar to those previously reported on other Virginia barrier islands (Dueser and Brown, 1980; Porter and Dueser, 1982; Dueser and Porter, 1986). Microhabitat analysis demonstrated that significant habitat selection was exhibited by all species during all seasons of the year. *Peromyscus* exhibited the least overlap with other species and they also failed to show a general increase in habitat overlap in winter as did other species. *Microtus* tended to occupy microhabitats in which monocot vegetation and abundant ground cover occurred. *Oryzomys* were most abundant in moist microhabitats and were locally abundant in tidal creek areas. *Mus* were abundant in the open habitat of the dune grassland and also occurred in shrub dominated habitats. *Cryptotis* were relatively common at open sites in the shrub-marsh edge habitat as well as in open microhabitats of the dune grassland area. The dune grid

had a greater variety of microhabitats and was the only grid on which all seven species of small mammals were captured. Although the specific descriptors for species occurrence differ between this study and prior studies, both characterize the same general habitats and the small mammal species were found in the same associations.

Schoener (1982, 1983) reviewed and evaluated the published evidence for strong competition in the formation of communities and found little evidence to support this conceptual hypothesis. He noted that most studies show that during the most restrictive seasons of a year the amount of interspecific overlap is reduced as the resident species specialize on particular resources. Although many prior studies on Virginia barrier islands suggest that interspecific competition is present, habitat selection always was a very significant variable. This study revealed that habitat selection by the small mammal species was always very strong and was present throughout the year. The degree of habitat overlap increased in the winter, and during that season the potential for competitive interactions was probably the greatest. The centroids for distribution of all species along the resource axes are distinct even though the total range of sites at which a species was captured may exhibit a fair degree of overlap. This study, as did that of Dueser and Porter (1986), produced evidence for habitat selection as a very strong force in determining the small mammal species diversity present in the different communities on this coastal barrier island.

ACKNOWLEDGEMENTS

This paper is dedicated to Mark Maly whose sudden accidental death cut short a promising career in mammalian ecology. His initial data stimulated me to continue the study beyond the first year in an attempt to address some of the questions he raised about the species assemblage on Assateague Island. I wish to thank Irvin Ailes (Chincoteague Wildlife Refuge biologist) for his help during the study period and Dr. R. D. Dueser for organizing the symposium from which this paper is derived.

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Ecology of Feral House Mice (*Mus musculus*) on Wallops Island, Virginia

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ABSTRACT

The ecology of feral house mice (*Mus musculus*) was studied on Wallops Island, Virginia, during August 1981, March and May 1982, and March 1983. Small mammal populations were sampled on live-trapping grids and snap-trapping transects which encompassed a variety of habitats on the north end of Wallops Island: strand, primary dunes, interdunes, secondary dunes, old dunes, grass meadow, grass-shrub association, *Myrica* thickets, and woodland. Six hundred and seventy-two small mammals representing five species were collected: 85 least shrews (*Cryptotis parva*), 51 white-footed mice (*Peromyscus leucopus*), 519 house mice, 13 meadow voles (*Microtus pennsylvanicus*), and 4 rice rats (*Oryzomys palustris*). *Mus musculus* was the numerically dominant species, comprising 74.9% of 370 specimens in August 1981; 88.8% of 89 specimens in March and 90.3% of 124 specimens in May 1982; and 57.3% of 89 specimens in March 1983. There was minimal spatial overlap in the distribution of *Mus* and *P. leucopus*. *Mus* exhibited a non-random pattern of habitat utilization during all sampling periods and on all grids and transects. They evinced a significant preference for primary dunes and were never taken in woods. Their overall pattern of habitat distribution was consistent with a hypothesis that *Mus musculus* on Wallops Island select habitats which presumably resemble natural habitats in which ancestral populations of this species evolved.

Key words: small mammals, ecology, barrier island, habitat utilization, house mouse, *Mus musculus*, white-footed mouse, *Peromyscus leucopus*.

INTRODUCTION

The introduced house mouse (*Mus musculus*) occurs throughout the United States, usually as a commensal with man but frequently as feral populations (Blair *et al.*, 1968; Hall, 1981). Very successful as a commensal, *Mus musculus* often does not do well in association with native North American species under natural conditions (Caldwell, 1964; Caldwell and Gentry, 1965; Lidicker, 1966; Sheppe, 1967; Whitaker, 1967; Briesse and Smith, 1973). Feral *M. musculus* populations may reach substantial densities either in the absence of native American species (Lidicker, 1966) or in association with native species in unstable agricultural habitats (Stickel, 1979). Small mammal communities in which *Mus musculus* was the numerically dominant species have been studied by Hall (1927) and Pearson (1964)

in California grasslands and by Dueser and Porter (1986) on Assateague Island, Maryland-Virginia. Because *M. musculus* can assume either a numerically subordinate or dominant position within individual small mammal communities, continued studies are needed to elucidate the conditions which determine its status within communities and its relationships with native species of small mammals.

In a survey of the mammals of the Virginia barrier islands, Dueser *et al.* (1979) collected *Mus musculus* on only 4 of 11 islands sampled. Although Bailey (1946) and Paradiso and Handley (1965) cite historical records of the occurrence of the native white-footed mouse (*Peromyscus leucopus*) on two Virginia barrier islands (Hog and Assateague), Dueser *et al.* (1979) failed to capture this species on any of the islands they sampled. Dueser and Porter (1986) subsequently captured *P. leucopus* on Cedar Island, which was not among those surveyed by Dueser *et al.* (1979). Another Virginia barrier island not sampled by Dueser *et al.* (1979) was Wallops Island, Accomack County. Preliminary sampling of small mammals on Wallops by the first author and his students during 1974 and 1975 confirmed the presence of both *Mus musculus* and *Peromyscus leucopus*. These two species appeared to exist in syntopy on the northeastern tip of Wallops Island. These preliminary observations suggested that Wallops Island was an appropriate site to study the spatial and numerical relationships of these two potential competitors, and in 1981 we initiated such a study. Our principal objectives were 1) to determine the ecological distribution of *M. musculus* on the north end of Wallops Island, and 2) to ascertain the numerical and spatial relationships between *M. musculus* and *P. leucopus* in the study area. In this paper we present data and results that are relevant to answering these two questions, and we propose a hypothesis to explain the observed pattern of habitat association evinced by *M. musculus* on Wallops Island.

METHODS AND MATERIALS

Small mammals were sampled on the north end of Wallops Island in August 1981, March and May 1982, and March 1983. Both live and removal sampling were employed. Live-trapping was carried out in August 1981 on two grids, one 7 x 10 stations and the other 6 x 12 stations. Assuming a boundary strip having a width equal to one-half the interstation interval of 15 m, these two grids had effective sampling areas of 1.58 ha and 1.62 ha, respectively. The grids were oriented so that they would sample a diversity of habitats extending inland from the strand. At each station, two Sherman live traps (one large - 7.5 x 9.0 x 23.0 cm and one small - 5.0 x 6.5 x 16.5 cm) baited with rolled oats were set within 1 m of the station marker. Each grid was run for a total of seven days but not concurrently. In order to prevent trap mortality owing to exposure to high daytime temperature, we closed all traps each morning (0700-0830 h) as we checked them and reopened all traps in the afternoon (1500-1700 h). Specimens captured were numbered by toe-clipping, measured (total, tail, and hind foot lengths), weighed, sexed, and released at the site of capture. At each trap station, the following habitat variables were recorded: general habitat, percentage of open sand and dead ground cover, percentage cover and average height of herbaceous and woody plants within a 2 m circle centered on the station marker.

In May 1982 the 6 x 12 station grid was re-established at approximately the same position (est. 90% + overlap) and was sampled for five days with the same methodology as employed in August 1981. For purposes of analysis, the May 1982 grid was considered to be coincident with the 6 x 12 station grid operated in August 1981. Accordingly, statistics such as the percentage of stations at which *Mus* and *Peromyscus* co-occurred on the live-trapping grids were based on a total of 142 stations (not 214).

Transects of snap traps (Museum Specials) were used during all study periods to augment data collected from the live-trapping grids. Transects varied from 33 to 50 stations with three traps set per station. Transects were oriented so as to sample the principal non-aquatic habitats on the northeast tip of Wallops Island. Each transect was operated for three days. At each trap station, the same categories of habitat data were recorded as at stations on the live-trapping grids. In March 1983, the 6 x 12 grid established in May 1982 was re-sampled using two Museum Special traps per station.

Population estimates for the live-trapping grids were calculated using the Schnabel technique (Smith 1980). The sample of *Mus musculus* was divided into three relative age classes using body mass as the aging criterion. Juveniles were defined as having body mass < 10 g; subadults, 10-18 g; and adults > 18 g. This represents a modification of the aging scheme of Rowe *et al.*, (1964) who defined adult *M. musculus* as having a body mass > 17.6 g; subadults, 12.6-17.6 g; and infants/juveniles < 12.6 g.

SITE DESCRIPTION

Wallops Island is located on the Atlantic side of the Delmarva Peninsula approximately 14 km south of the Maryland-Virginia border. The island is the site of a launch facility of the National Aeronautics and Space Administration (NASA). Buildings and other NASA structures are confined largely to the southern two-thirds of the island. An abandoned U.S. Coast Guard Station is located on the mainland side of the north end. At present, there is no resident human population on Wallops Island.

The northeastern tip of Wallops Island supports a complex mosaic of vegetation (Klotz, 1986). Small mammals were sampled in nine habitats: strand, primary dunes, interdunes, secondary dunes, grass-shrub association, old dunes, *Myrica* thickets, grass meadow, and woodland. A foredune strand zone of variable width (10-40+ m) supports sparse vegetation, primarily sea-rocket (*Cakile edentula*), saltwort (*Salsola kali*), and seaside goldenrod (*Solidago sempervirens*). Inland the strand is bordered by primary dunes which are dominated by the grasses *Ammophila breviligulata* and *Panicum amarum* but also support some forbs, such as seaside goldenrod. Well-defined secondary dunes are present on the southern one-third of the study area. Vegetationally these are distinguished from primary dunes by denser living ground cover, the dominance of salt meadow cordgrass (*Spartina patens*), the presence of several woody species, most notably Virginia creeper (*Parthenocissus quinquefolia*) and poison ivy (*Rhus radicans*), and additional forbs, such as horsemint (*Monarda punctata*). Lying between the primary and secondary dunes, the interdune habitat is influenced by overwash during storms and supports an herbaceous community of grasses (e.g., *Ammophila breviligulata*

and *Spartina patens*) and forbs, such as horsemint and seaside goldenrod. Towards the northern end of the study area, the interdune-secondary dune complex is absent and is replaced by a broad (100-200 m wide) level expanse of grassland, *Myrica* thickets, and admixtures of these two habitats (grass-shrub association). The grassland habitat is virtually devoid of woody species and is dominated by *Spartina patens* but also supports forbs such as sea-pink (*Sabatia stellaris*) and seaside goldenrod. Two species of *Myrica* are present, bayberry (*M. pensylvanica*) and wax-myrtle (*M. cerifera*); however, owing to their similarity, we did not attempt to distinguish between them in our habitat analysis. *Myrica* spp. occur either as scattered individuals interspersed with grasses (grass-shrub habitat) or in well-defined stands 3-5 + m across (*Myrica* thicket habitat). These thicket habitats are largely devoid of living ground cover, especially in comparison to the grassland and grass-shrub habitats. In the grass-shrub habitat, the *Myrica* spp. are generally 2-3 m in height, whereas in the *Myrica* thickets they are 3-5 m in height. Groundsel-tree (*Baccharis halimifolia*) is the other principal woody species in the grassland-thicket habitat. Old dunes are small unstable areas of fairly high relief within the grassland-thicket associations. Although old dunes support the same grasses as the primary dunes, they are characterized by sparser vegetation and the presence of bare sand caused by "blowouts." The interior of the northeast tip of Wallops Island supports woods dominated by loblolly pine (*Pinus taeda*), *Myrica* spp., cherry (*Prunus serotina*), and sassafras (*Sassafras albidum*). Common ground cover species in woodland habitats are poison ivy and greenbriar (*Smilax* spp.). The ecotone between the forests and open herbaceous habitats is characterized by dense stands of *Myrica* spp. and dwarf sumac (*Rhus copallina*).

RESULTS

Five species of small mammals were collected in the study area: the least shrew (*Cryptotis parva*), white-footed mouse (*Peromyscus leucopus*), rice rat (*Oryzomys palustris*), meadow vole (*Microtus pennsylvanicus*), and house mouse (*Mus musculus*). The house mouse was by far the most abundant of the five species throughout the study. In the four sampling periods it comprised from 57.3 to 90.3% of small mammals, and overall, *Mus* constituted 77.2% of the 672 specimens captured (Table 1). The least shrew was the second most abundant small mammal on our study sites during August 1981, comprising 21.9% of the total sample; however, it declined dramatically in abundance over the winter of 1981-82 and was seldom taken during subsequent sampling (Table 1). The relatively high proportion of *Peromyscus leucopus* in the March 1983 sample (32.6%) reflects the sampling of two wooded sites, which yielded 28 of 29 *P. leucopus* taken during that period (Table 1). Marsh habitats were not extensively sampled, and this may explain the low numbers of *Oryzomys* and *Microtus* taken (Table 1). Both species are common to abundant in salt and brackish marsh habitats on Wallops Island and the adjacent mainland (Kirkland unpublished data) and on Assateague Island (Cranford and Maly, 1990).

In the three live-trapping samples, *Mus* had estimated densities of 48.5 to 59.9/ha and comprised 77.1 to 89.4% of the small mammals trapped (Table 2). The percentage of stations at which *Mus* were captured ranged from 53.8 to 88.4% during the three sampling periods. The clumped nature of the distributions of *Mus*

TABLE 1. Summary of small mammal captures (N) on Wallops Island, Virginia, based on live- and snap-trapping (1981 - 1983).

| SPECIES | AUGUST 1981 | | MARCH 1982 | | MAY 1982 | | MARCH 1983 | | OVERALL | |
|--|-------------|------|------------|------|----------|------|------------|------|---------|------|
| | N | % | N | % | N | % | N | % | N | % |
| Least Shrew <i>Cryptotis parva</i> | 81 | 21.9 | 1 | 1.1 | 1 | 0.8 | 2 | 2.3 | 85 | 12.7 |
| Rice Rat <i>Oryzomys palustris</i> | 1 | 0.3 | - | - | 2 | 1.6 | 1 | 1.1 | 4 | 0.6 |
| White-footed Mouse <i>Peromyscus leucopus</i> | 9 | 2.4 | 5 | 5.6 | 8 | 6.5 | 29 | 32.6 | 51 | 7.6 |
| Meadow Vole <i>Microtus pennsylvanicus</i> | 2 | 0.5 | 4 | 4.5 | 1 | 0.8 | 6 | 6.7 | 13 | 1.9 |
| House Mouse <i>Mus musculus</i> | 277 | 74.9 | 79 | 88.8 | 112 | 90.3 | 51 | 57.3 | 519 | 77.2 |
| Totals | 370 | | 89 | | 124 | | 89 | | 672 | |

TABLE 2. Summary of live-trapping results from Wallops Island, Virginia.

| SPECIES | August 1981 | | May 1982 |
|--|-------------|-------------|-------------|
| | 7 x 10 Grid | 6 x 12 Grid | 6 x 12 Grid |
| <i>Cryptotis parva</i> | 6 | 25 | 0 |
| <i>Oryzomys palustris</i> | 0 | 0 | 2 |
| <i>Peromyscus leucopus</i> | 3 | 4 | 7 |
| <i>Microtus pennsylvanicus</i> | 0 | 0 | 1 |
| <i>Mus musculus</i> | 76 | 101 | 63 |
| Totals (Individuals Captured) | 85 | 131 | 73 |
| % House Mice | 89.4 | 77.1 | 86.3 |
| # Stations at which House Mice Captured | 50 | 64 | 42 |
| % Stations at which House Mice Captured | 71.4 | 88.4 | 53.8 |
| S ² / \bar{X} -Ratio House Mice | 1.78 | 1.71 | 1.71 |
| Density: House Mice/ha | 48.5 | 59.9 | 55.4 |

on the three grids was further evidenced by variance/mean ratios of captures at trap stations that ranged from 1.71 to 1.78 (Table 2). A similar pattern of clumping of captures was evident in the snap-trapping data. Excluding data from two forest transects which yielded no house mice, *Mus* were taken at 108 of 250 or 43.2% of the stations on the six transects. The variance/mean ratios for *Mus* captures on these transects ranged from 1.49 to 2.72.

These clumped patterns of dispersion suggested that *Mus* preferred some habitats and were captured in these at higher frequencies than expected by chance while they tended to avoid other habitats. To ascertain this, we analyzed the habitat association of *Mus* in the eight habitats present on the live-trapping grids based on 825 total captures of 240 individuals. Chi-square analyses, comparing the observed captures of house mice in individual habitats versus expected captures based on the proportional sampling effort in each habitat, revealed highly significant deviations from the expected in the entire sample of *Mus musculus*, as well as in each of three relative age classes (Table 3). The data for the entire sample, as well as the individual age classes, revealed a higher than expected percentage of captures in the primary dunes. Although there was some variation among the age classes in the proportional catch in each habitat (Table 3), a Kendall Coefficient of Concordance ($W = 0.824$; Siegel 1956) revealed significant agreement among the rankings ($p < 0.02$) of the three age classes.

Spatial overlap between *Mus musculus* and *Peromyscus leucopus* on the study area was minimal. On the live-trapping grids, both species were taken at 12 of 142 or 8.5% of the stations. On eight snap-trapping transects having a total of 300 stations, both species were taken together at only two or 0.67% of the stations. Of the 14 total stations at which both species were taken (combined live- and snap-trapping), their distribution by habitat was: myrtle thickets (7), grass-shrub (5), grass meadow (1), and old dune (1). *Mus* and *Peromyscus* were segregated largely on the basis of wooded versus non-wooded habitats. On Wallops Island, *Mus* were never taken in the wooded habitats sampled, while 31 of 38 *P. leucopus* taken in the snap-trapping transects were from wooded habitats. The positive association between *Peromyscus* and woody habitats extended to the live-trapping grids, where the 31 captures of 14 individuals were limited to 12 stations, 7 of which were in myrtle thickets. On the live-trapping grids, only 12 of 142 stations (8.5%) were characterized by myrtle thickets. Thus, *Peromyscus* were taken at 58.3% (7 of 12) of the stations at which this spatially limited habitat occurred.

DISCUSSION

Our results, with respect to the abundance and ecological distribution of *M. musculus*, differed substantially from those of Shure (1970), who studied small mammals on an Atlantic coastal island in New Jersey. In that study, *Mus* comprised only 2.7% (29 of 1069) of the specimens collected in a five-species community which also included *P. leucopus* (489), *M. pennsylvanicus* (317), *Zapus hudsonius* (196), and *Sorex cinereus* (38). Although *Mus* were most frequently captured in herbaceous habitats on the New Jersey island, they were not most abundant in dunegrass habitat. *Mus* were largely absent from mixed herb-shrub habitats in Shure's study, whereas they were common to abundant in these habitats on Wallops Island (Table 3). In New Jersey, all of these habitats supported large populations of *P. leucopus*. The difference between Shure's and our results may be related to habitat differences between the two study areas and the impact these may have had on the abundance and interspecific relationships of resident species. For example, in view of the relatively high moisture requirements of *M. pennsylvanicus* and *Z. hudsonius*, and their preference for sites characterized by high soil moisture and rank vegetation (Getz, 1961a, 1961b), the presence of large numbers of these

TABLE 3. Analysis of habitat distribution of house mice on live-trapping grids on Wallops Island, Virginia. Chi-square analysis was performed on numbers of captures in each habitat, with expected values based on sampling effort in each habitat.

| HABITAT | Percent Sampling Effort | Percent Total Catch of House Mice | | | |
|-----------------------|----------------------------|-----------------------------------|-----------|-----------|--------|
| | | Overall | Juveniles | Subadults | Adults |
| Strand | 17.0 | 15.2 | 12.8 | 19.6 | 10.8 |
| Primary Dunes | 16.4 | 28.6 | 19.8 | 36.6 | 25.5 |
| Interdunes | 5.8 | 5.1 | 10.3 | 4.5 | 0.4 |
| Secondary Dunes | 4.2 | 1.9 | 3.7 | 1.7 | 0.4 |
| Grass/Shrub Assoc. | 33.0 | 31.9 | 37.2 | 25.0 | 36.8 |
| Old Dunes | 8.2 | 5.5 | 4.5 | 3.4 | 9.5 |
| <i>Myrica</i> Thicket | 7.4 | 5.5 | 2.5 | 4.5 | 10.0 |
| Grass Meadow | 8.0 | 6.4 | 9.1 | 4.5 | 6.5 |
| Totals (Captures) | | 825 | 242 | 352 | 231 |
| X ² | | 101.41* | 26.45* | 121.55* | 40.45* |

* $P < 0.001$

species at the New Jersey site suggests that it was substantially moister than our study areas on Wallops Island, which yielded only 13 *M. pennsylvanicus* (and no *Zapus*). Also, as reported by numerous authors, *Mus musculus* tends to be uncommon to absent in wooded habitats (Whitaker, 1968; Zejda, 1975). One conspicuous exception is New Zealand, where *Mus* is common in southern beech (*Nothofagus*) forests (King, 1982).

Research by Porter and Dueser (1982) and Dueser and Porter (1986) on habitat selection and competition in small mammals on Assateague Island permit comparison of our results with those of another island in the Maryland-Virginia barrier island complex. Cranford and Maly (1990) provide additional insights into the habitat relationships of small mammals on Assateague Island, which lies approximately 2 km NNE of Wallops and from which it is separated by Chincoteague Inlet. With a length of about 60 km and an approximate area of 7029 ha (Porter and Dueser, 1982), Assateague is about five to six times the size of Wallops, which is 11 km long (Klotz, 1986) and encompasses 1214 ha (ca. 3000 ac.; Turgeon and Turgeon, 1980). Owing to the larger size of Assateague, it is not surprising that it supports at least one additional species of native small mammal, the meadow jumping mouse (*Zapus hudsonius*), which comprised 16.7% of the individuals collected by Dueser and Porter (1986) but only 4.6% of the individuals in Cranford and Maly's (1989) sample of 567 small mammals. Although *Mus* was also the numerically dominant small mammal in Dueser and Porter's (1990) sample from Assateague, it constituted only 43.1% of the total (196 of 455) compared to 77.2% in our Wallops sample (Table 1). In Cranford and Maly's study, *Mus* was the third most abundant species (after *Microtus pennsylvanicus* and *Oryzomys palustris*) and comprised 22.6% of their sample. This variation may reflect differences in proportions of habitats sampled in these studies. Nevertheless, these studies reveal similar results regarding habitat selection by *Mus* and the potential interspecific interactions of *Mus* and *P. leucopus*. The negative spatial and numerical relationships between *Mus* and *P. leucopus* observed in our Wallops Island data were also evident

on Assateague. Cranford and Maly (1990) found limited spatial overlap of *Mus* and *Peromyscus* and a preference in the latter for wooded habitats. Porter and Dueser's (1982, Fig. 1) depiction of the habitat of *Mus* in discriminant space on Assateague suggests a preference for sites having low herbaceous cover and relatively low shrub cover. In our study, sites yielding *Mus* had mean herbaceous cover of 52.5% within 2 m of the trap and only 2.7% shrub cover. Sand (39.3%) and organic litter (5.2%) formed the remainder of surface area at such sites. The discriminant habitat profile of *P. leucopus* on Assateague showed it to be differentiated from *Mus* in terms of its preference for sites with dense shrub cover (Porter and Dueser, 1982). In addition to exhibiting a pattern of spatial segregation on Assateague, *Mus* and *Peromyscus* also evinced significant competition coefficients (Porter and Dueser, 1982).

Given the fact that house mice on Wallops Island appear to select certain preferred habitats and reduce their utilization of others, we are faced with the question of why they exhibit the pattern they do? As noted above, avoidance of wooded habitats by *M. musculus* is typical. Whether this represents inherent habitat selection or is the result of competitive interactions with native forest-dwelling small mammals cannot be determined on the basis of our Wallops Island data. B. J. Fox (pers. comm.) notes that although *Mus musculus* occurs throughout Australia, it is absent from rainforest habitats. Strahan (1983) suggests that the absence of feral populations of *Mus musculus* in northern tropical Australia may be the result of the competitive superiority of larger native forest-dwelling species of *Rattus* and *Melomys*. However, during our field work on Wallops Island, the abundance of *P. leucopus*, the principal potential native competitor of *Mus* in the wooded habitats, was low, averaging 3.1 captures/100 trap nights. Given the relatively low numbers of *P. leucopus* in wooded habitats on Wallops during our study, the overwhelming numerical dominance of *Mus musculus* in non-wooded habitats on the island is inconsistent with their being forced into such habitats as a result of interspecific competition with *P. leucopus*. The fact that Dueser and Porter (1986) determined that *P. leucopus* was competitively superior to *Mus* on Assateague Island suggests that site characteristics of individual study areas may influence the perceived competitive interactions between species.

In contrast to most populations of house mice which live in close association with man and his structures, the Wallops Island population is truly feral and free-ranging. It provides us with an opportunity to observe habitat selection in this species under conditions of minimal influence by man. We propose that the observed habitat distribution of *Mus musculus* on Wallops Island can be explained on the basis of its evolutionary history prior to becoming a commensal with man. *Mus musculus* presumably originated in the semi-arid regions east of the Caucasus Mountains of Asia and physiologically is well adapted to survive arid conditions (Watts and Aslin, 1981). Schwarz and Schwarz (1943) reported that all wild forms of *Mus musculus* are typically residents of dry regions, inhabiting savannahs, steppes, and occasionally deserts. Watts and Aslin (1981) note that like many small desert rodents, house mice avoid the heat of the day by living in burrows and becoming active principally at night, thus conserving water. On Wallops Island, the vast majority of snap-trapped *Mus* were taken during the night. On the live-trapping grids, released *M. musculus* frequently ran immediately to and entered

burrows which they shared with ghost crabs (*Ocypode quadratus*). Thus, in some aspects of their behavioral repertoire, Wallops Island house mice resemble desert-dwelling *Mus musculus*.

The principal habitat of *Mus musculus* on Wallops Island was primary dunes. Based on a sample of 82 trap stations, primary dunes on Wallops were characterized by means of 53.8% living ground cover, 41.3% sand cover, and 4.9% organic litter, with herbaceous species dominated by grasses which comprised 95.3% of the living ground cover. We propose that of the available habitats on the north end of Wallops Island, primary dunes are the most similar to those of ancestral wild forms of *Mus musculus*, and we therefore hypothesize that on Wallops Island, the habitat distribution of *Mus musculus* reflects a preference for that habitat which most closely resembles the ancestral habitats of this species.

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Den Site Characteristics and Food Habits of the Red Fox (*Vulpes vulpes*) on Assateague Island, Maryland

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ABSTRACT

Aerial searches and ground surveys were used to locate red fox (*Vulpes vulpes*) excavations on Assateague Island, Maryland. Aerial searches were not successful since excavation entrances were concealed by vegetation and shadows from sand dunes. Red fox excavations on Assateague Island were located predominantly in shrub succession and *Hudsonia* dune habitats. Sand dunes within these habitats provided suitable denning sites. Average height and width measurements of fox excavations were significantly smaller in 1987 compared to 1985. These differences may be related to an increase in the number of juveniles. In 1985 and 1987, red fox excavations were predominantly oriented towards the northeast and northwest quadrants. Number of red fox denning areas increased from an estimated 8 to 11 between 1985 and 1987. Although the number of denning sites increased, the average distance between centers of denning areas decreased by 0.8 km. Red foxes on Assateague Island had a typically varied diet during summer 1987. Major components of the red fox diet as revealed by scat analysis included mammals (87.0%), crustaceans (64.8%), and birds (46.3%). Among the mammals, eastern cottontail rabbits (*Sylvilagus floridanus*) had the highest frequency of occurrence followed by meadow voles (*Microtus pennsylvanicus*) and white-footed mice (*Peromyscus leucopus*).

Key words: Red fox, *Vulpes vulpes*, Assateague Island, barrier island, denning habits, aerial searches.

INTRODUCTION

"Red fox are so variable in their behavior that any extrapolations leading to the management of foxes in one area based on studies from another should be viewed with caution" (Voigt and Macdonald, 1984). This statement based on the comparisons of red fox (*Vulpes vulpes*) populations in England and Canada, demonstrates the need for research to be conducted on individual red fox populations before developing management programs.

On 1 January 1985 the National Park Service prohibited trapping of red foxes within Assateague Island National Seashore, Maryland. Chincoteague National Wildlife Refuge, located just south of the Maryland/Virginia border (Fig. 1) still maintains a red fox trapping season. A study was initiated during summer 1985 to estimate the size of the red fox population on Assateague Island. Due to the

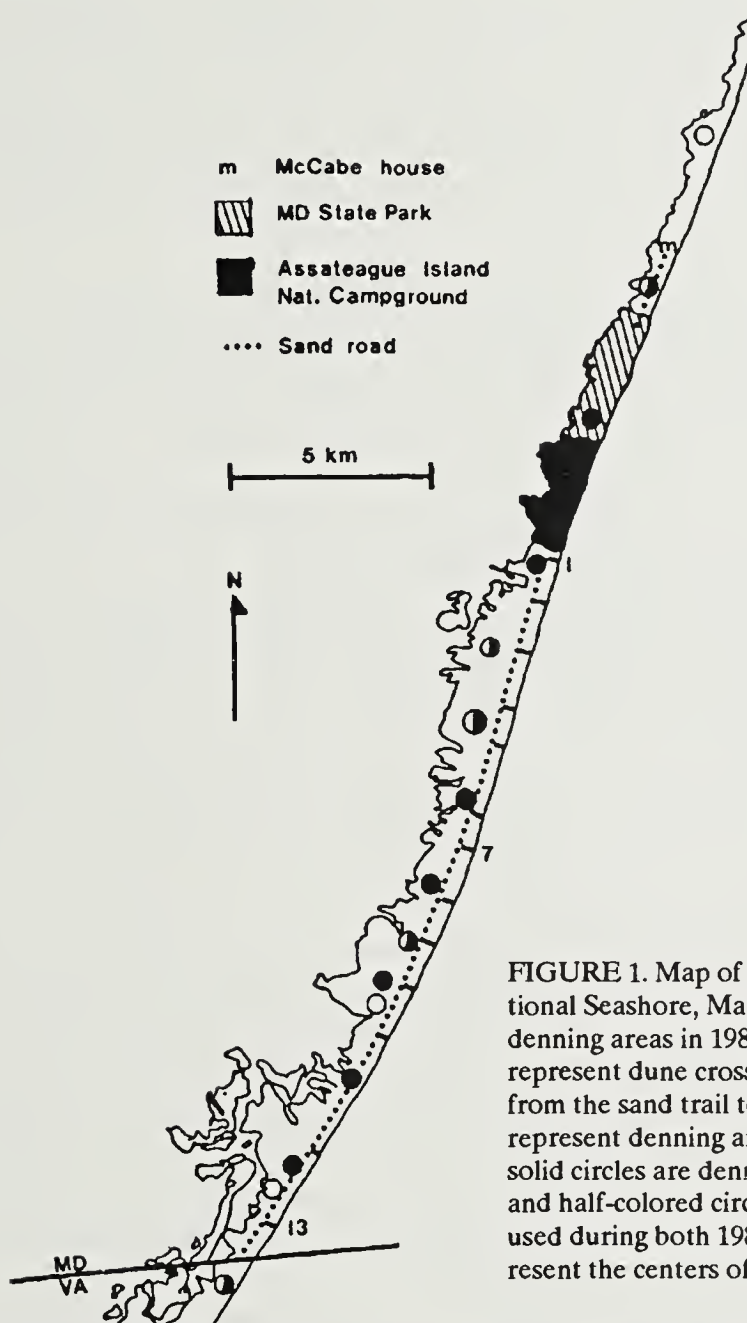


FIGURE 1. Map of Assateague Island National Seashore, Maryland showing red fox denning areas in 1985 and 1987. Numbers represent dune crossings permitting access from the sand trail to the beach. Open circles represent denning areas from 1985, while solid circles are denning areas used in 1987, and half-colored circles are denning areas used during both 1985 and 1987. Circles represent the centers of denning areas.

absence on Assateague Island of mortality factors, such as farm machinery, highways, and predation (Storm *et al.*, 1976; Pils and Martin, 1978), we believed this population would increase after trapping ceased.

These studies were undertaken in order to augment existing knowledge on the Assateague Island red fox population and to help the National Park Service formulate a management plan for this species. In this paper den-site characteristics and population estimates from two study years were compared to evaluate changes in these aspects of insular red fox ecology. In addition, we report on the first analysis of fox food habits from the Atlantic barrier islands.

STUDY AREA

The study area consisted of 25.4 km² of Assateague Island National Seashore, Worcester Co., Maryland. The study area extended from Ocean City Inlet on the northern end of Assateague Island southward 0.8 km beyond the Virginia border,

and included 0.4 km² of the Chincoteague National Wildlife Refuge, immediately south of the State Line (Fig. 1). This area is bounded by the Atlantic Ocean on the east, and Chincoteague and Sinepuxent bays on the west. From east to west across the island the typical sequence of terrestrial communities was: high energy beach, primary dunes, *Hudsonia* dunes, shrub succession, pine woods, and wetlands, with fresh water ponds interspersed within individual communities in the interior of the island (Hill, 1986).

MATERIALS AND METHODS

The first year of the study extended from 20 May to 18 August 1985, while the second year extended from 20 May until 30 August 1987. Five low level (approximately 30.5 m above M.S.L.; 70 ± 10 kts.) aerial searches to locate red fox excavations were flown during April (1), May (3), and August (1) 1985. Flights were made in a Cessna-150 by a pilot and one observer, who was experienced with the appearance of fox excavations. Two transect paths were flown per flight; North to South and South to North over the entire study area.

Ground surveys were undertaken by one to six people to locate fox excavations throughout the study area between 20 May - 23 July 1985 and 20 May - 20 July 1987. Survey and measurement techniques were identical in both years. Excavations were considered active based on the presence of fox tracks and whether the entrance was cleaned out (Sheldon, 1950). Excavations were further classified as dens (depth > 1.0 m), pseudo-dens (depth 0.5-1.0 m), and digs (depth < 0.5 m) (Bashore and Krim, 1986). Only dens and pseudo-dens were analyzed in this study, because digs were usually related to caching or other non-denning activities. Orientation of entrance openings (in degrees) was determined by using a Warren-Knight forester's compass. Hourly records of wind speed and direction for both 1985 and 1987 were obtained from NASA, Wallops Island, Virginia, 32 km southwest of Assateague Island. Entrance height and width were measured using expandable kitchen corn tongs. These were inserted 45 cm into the opening, expanded to the height or width of the tunnel, held in position as they were extracted, and placed on a meter stick to obtain measurements. The 45 cm depth was chosen to minimize bias caused by sand blown into or fallen at the entrance. Collapsed excavations could not be measured.

In North America, red fox families traditionally consist of a pair of foxes (one adult male and female) and their pups, and occupy well-defined contiguous territories (Scott, 1943). Sargeant *et al.* (1975) assigned dens within 1.6 km of each other to the same fox family. Bashore and Krim (1986) defined a red fox denning area as a section of Assateague Island which contained at least one active den in association with other dens, pseudo-dens, and digs. Denning areas were identified by plotting fox excavations on vegetation maps. When plotted, these excavations often took the form of distinctive clusters, which usually occurred within 1.6 km of each other. Denning areas lacking distinct clusters were determined by drawing a circle (1.6 km in diameter) from the center of a major group of excavations.

In 1987, relative coverage of open ground, grasses and forbs, shrubs, and trees was estimated for a 10 m radius circle centered on the excavation. This was determined by running four transect lines (10 m in length) from the excavation opening, and were oriented to cover the four ordinal directions. The length of

transect passing under the dripline of a tree was measured to determine relative coverage of trees. The portion of transect length intercepted by plants or by a perpendicular projection of their foliage was measured for grasses, forbs, and shrubs. The amount of open ground (non-vegetated) which intercepted the transect also was measured (Brower and Zar, 1977).

All excavations from the two years were plotted on a vegetation map (1:8640 scale) (Hill, 1984) and on a U.S. Department of Agriculture Soil Survey map (1:15840 scale) (Hall *et al.*, 1973). Chi-square tests were performed to determine if red fox excavations were distributed randomly among seven habitat types. To compute expected values, the areal percent for each habitat was multiplied by the total number of excavations located. To meet the assumptions of the chi-square test (Zar, 1984), two habitat types (non-vegetated plus washes and pans) were combined.

Red fox scat collected between May - August 1987 was analyzed to determine food habits. The scat was washed and broken up, floated in a sieve of clean water to separate it further and dried at 50° C for at least 24 hours (Lockie, 1959; Green *et al.*, 1986). Scat contents were separated into eight major categories: mammals, birds, crustaceans, fish, insects, plants, molluscs, and unknown. Where possible mammal remains were identified to genus or species by analyzing bone fragments, teeth, and hair present in the scat.

Statistical analyses followed the procedures of Zar (1984) and were performed using BIOSTAT I (Pimentel and Smith, 1985).

RESULTS

Three potential fox excavations were observed during the two afternoon flights and no sightings occurred during morning flights. One sighting was verified as a shallow dig (depth < 50 cm) in a sparsely vegetated sand dune. The second possible excavation was not located during a ground search four days later, while the third sighting was verified as a previously located pseudo-den in a sparsely vegetated primary dune.

In 1985, 61 red fox excavations were located from ground searches. Of these, 49 (80.3%) were classified as dens (16 active; 33 inactive) and 12 (19.7%) were pseudo-dens (3 active; 9 inactive). In 1987, 96 fox excavations were located. Of these, 70 (72.9%) were classified as dens (41 active; 29 inactive) and 26 (27.1%) were pseudo-dens (6 active; 20 inactive). Pseudo-dens were found both in association with dens and other pseudo-dens and isolated from other fox excavations. Dens and pseudo-dens with one opening were common on Assateague, 43 of the 61 excavations in 1985 and 75 of 96 excavations in 1987 had only one opening.

Height and width measurements of fox excavations from 1985 were compared to those from 1987 (Table 1). Some excavations had collapsed before height and width measurements could be made. Active pseudo-dens were not analyzed due to small sample sizes in both 1985 ($n = 3$) and 1987 ($n = 4$). There were significant differences between years in the heights and widths of all three excavation types (active and inactive dens, and inactive pseudo-dens), with sample means in 1987 smaller than those in 1985. Average height and width dimensions of active dens in 1985 were 23 x 25 cm and in 1987 were 20 x 22 cm. In 1985, 32 (54.2%) excavations were oriented towards the northwest, 14 (23.7%) faced southwest, 12 (20.3%) faced

northeast, and 1 (1.7%) faced southeast. In 1987, fox excavations were oriented predominantly towards the northeast ($n = 34$; 36.9% of the total) and northwest (29; 31.5%), with fewer being oriented toward the southwest and southeast (19; 20.7% and 10; 10.9%, respectively). Directional orientation of excavations differed significantly between 1985 and 1987 ($X^2 = 12.25$, $P < 0.01$). Between 1985 and 1987 there was a significant increase in the frequency of excavations oriented towards the southeast ($Z = -3.54$, $P < 0.01$). However, in 1987, 68.4% of the excavation entrances were oriented towards the northeast and northwest quadrants. No significant correlations were observed between wind direction and excavation orientation or between winds above 20 mph, representing major storms, and excavation openings in either 1985 or 1987.

In 1985, 31 excavations were located in shrub succession, 19 in *Hudsonia* dune habitat, 7 in dunegrass and 1 in woodland communities. A Chi-square analysis was not performed on the data from 1985 because after combining two habitat types, the data still did not conform to the assumptions of the Chi-square test (Zar, 1984) (*i.e.* more than 20% of expected frequencies were less than 5.0). Fox excavations were distributed non-randomly among habitat types in 1987 (Table 2) ($X^2 = 781.8$, $df = 6$, $P < 0.001$). Of the 96 excavations located, 59 were in the *Hudsonia* dune habitat, with 31 in shrub succession, while woodland and dunegrass communities supported fewer numbers (4 excavations, and 2 excavations, respectively). In order to meet the assumptions of the Chi-square test (Zar, 1984), data from two similar habitats having small numbers of excavations (non-vegetated plus washes and pans) were combined. Between 1985 and 1987 there was a significant increase in the use of *Hudsonia* dune habitat for red fox excavation location ($Z = -2.30$, $P < 0.05$). There was also a corresponding significant decrease ($Z = 1.73$, $P < 0.05$) in red fox use of shrub succession habitat for excavation location.

There were an estimated eight breeding pairs of foxes (16 individuals) on Assateague Island in 1985. This increased to an estimated 11 pairs (22 individuals) in 1987. Because Assateague is a narrow barrier island oriented parallel to the coasts of Maryland and Virginia, denning sites were located from north to south in basically a straight line (Fig. 1). Therefore, measurements between the centers of adjacent denning areas were made continuously from north to south. The average distance between centers of adjacent denning areas decreased from 3.4 km in 1985 to 2.6 km in 1987.

In 1985, 51 excavations (83.6% of the total) were located in soils with a dominant sandy texture (coastal beach soils), while 9 excavations (14.8%) were in soil with a loamy sand texture (klej soil). During 1987, 93 excavations (96.9% of the total) were located in sandy soils, while 3 excavations (3.1%) were found in a soil with a sandy loam texture. There was a significant increase in the use of sandy textured soil for the location of fox excavations from 1985 to 1987 ($Z = -2.42$, $P < 0.01$).

Results from the analysis on the amount of barren ground and vegetative cover surrounding fox excavations were varied (Table 3). Open ground and shrubs were the only ground covers which showed significant differences among the different excavation types. ANOVA tests were performed on the average length of transect intercepted by barren ground and vegetative covers, while percent cover is recorded in Table 3. Although ANOVA tests revealed significant differences, the

TABLE 1. Comparison of average height and width measurements (in cm) of red fox excavations within Assateague Island National Seashore, Maryland, from 1985 and 1987. Active pseudo-dens from 1985 and 1987 were not included in the analysis due to the small sample sizes (3 and 4, respectively).

| Excavation Type | 1985 | 1987 | Statistic |
|----------------------|----------------|----------------|------------------------|
| Active Dens | | | |
| Height | 23 (n = 13) | 20 (n = 32) | U = 288 P < 0.05 |
| Width | 25 (n = 13) | 22 (n = 32) | t = 2.116 P < 0.05 |
| Inactive Dens | | | |
| Height | 19 (n = 15) | 17 (n = 17) | t = 2.593 P < 0.02 |
| Width | 25 (n = 15) | 21 (n = 17) | U = 192 P < 0.02 |
| Active Pseudo-dens | | | |
| Height | 23 (n = 3) | 25 (n = 4) | |
| Width | 23 (n = 3) | 27 (n = 4) | |
| Inactive Pseudo-dens | | | |
| Height | 24 (n = 9) | 16 (n = 10) | t = 3.820 P < 0.002 |
| Width | 27 (n = 9) | 20 (n = 10) | t = 4.227 P < 0.001 |

results of multiple range tests were ambiguous. In analyzing the amount of shrub cover, active and inactive dens, as well as active pseudo-dens grouped together, however, inactive dens and active pseudo-dens also grouped with inactive pseudo-dens. This could have resulted from the low sample sizes in both active and inactive pseudo-dens (4 and 19, respectively). The amount of open ground showed less ambiguity. Inactive pseudo-dens grouped with inactive dens and active pseudo-dens, but active dens also grouped with active pseudo-dens. Again this could be the result of only having four active pseudo-dens in the analysis.

Prey remains were often observed in the vicinity of red fox excavations. The most common prey item was the eastern cottontail rabbit (*Sylvilagus floridanus*), although skate (*Raja erinacea*) and blue fish (*Pomatomus saltatrix*) were fairly common. The skate and bluefish were probably left on the beach by fishermen and scavenged by foxes. A pony (*Equus caballus*) leg was also discovered outside a fox den, most likely from a carcass found by the foxes. Remains of other prey items found at fox excavations included muskrat (*Ondatra zibethicus*), meadow vole (*Microtus pennsylvanicus*), and willet (*Catoptrophorus semipalmatus*).

Based on the analysis of 56 scats, the diet of red foxes on Assateague Island, during the 1987 study, consisted primarily of mammals, crustaceans, and birds (Table 4). Of the identified mammals consumed, the eastern cottontail rabbit had the highest frequency of occurrence (44.4%), followed by the meadow vole (31.5%) and white-footed mouse (*Peromyscus leucopus*) (24.1%). From field observations

TABLE 2. Number and distribution of red fox excavations among habitats on Assateague Island National Seashore, Maryland from 1985 and 1987. Aerial extents of each habitat are from Bashore and Krim (1986). Numbers in parentheses are percent of total yearly sample.

| Habitat Type | 1985 | 1987 | Percent of Total Area |
|------------------------------------|--------------|--------------|-----------------------|
| Shrub succession | 31 (50.8) | 31 (32.3) | 15.3 |
| <i>Hudsonia</i> dunes | 22 (36.1) | 59 (61.5) | 4.5 |
| Dune grass | 7 (11.5) | 2 (2.1) | 10.0 |
| Woodland | 1 (1.6) | 4 (4.2) | 6.7 |
| Fresh water marsh | 0 | 0 | 14.9 |
| Tidal marsh | 0 | 0 | 35.4 |
| Non-vegetated plus Washes and Pans | 0 | 0 | 13.2 |
| Totals | 61 | 96 | |

during summers 1985 and 1987, rabbits appeared abundant on the island. The status of the meadow vole and white-footed mouse was unknown during this study.

DISCUSSION

Aerial surveys were not useful for locating red fox excavations on Assateague Island because most excavation entrances were concealed by vegetation or dune shadows. All fox excavations on Assateague Island were believed to have been dug by red foxes. This is in contrast with Pils and Martin (1978), who noted that red foxes in Wisconsin modified dens dug by badgers and woodchucks.

In 1987, both adult and juvenile red foxes were flushed from pseudo-dens; however, no foxes were flushed from excavations in 1985. Pseudo-dens may function as resting places for both adults and juveniles. Scott (1943) reported that red foxes in the northern Great Plains utilized nearby dens as outlying retreats, and Kolosov (1935) found that 70% of dens located in Russia were temporary retreats. These were shallow, short excavations having few, if any, branches and may have been similar to pseudo-dens found on Assateague.

There were significant differences between years in the heights and widths of all excavations types, with means in 1987 smaller than those in 1985. These differences may be related to the fact that more juveniles foxes were observed in 1987 compared to 1985. The average dimensions in 1987 were smaller than those reported by Storm *et al.*, (1976) in Illinois (28 x 23 cm), and in Iowa (25 x 23 cm), and by Pils and Martin (1978) in Wisconsin (28 x 23 cm). These differences may also be related to an increase in juveniles in 1987. More juveniles seen in 1987 may indicate a shift in the age structure of the population.

Directional orientations of red fox excavations differed significantly between 1985 and 1987. Although there was a significant increase in the frequency of

TABLE 3. Percentage composition of vegetative cover surrounding red fox excavations on Assateague Island National Seashore, Maryland in 1987. Letters represent results of multiple range tests and encompasses values that did not differ statistically ($P < 0.05$).

| Excavation Type | Open | Grass | Shrub | Tree |
|----------------------------------|--------|-------|-------|------|
| Active Dens (N = 34) | 56.9a | 31.8 | 10.9a | 0.4 |
| Active Pseudo-Dens (N = 4) | 47.4ab | 23.3 | 27.7a | 0.8 |
| Inactive Dens (N = 27) | 44.3b | 30.6 | 23.1a | 2.0 |
| Inactive Pseudo-Dens (N = 19) | 41.7b | 27.6 | 29.9 | 0.8 |

excavations oriented towards the southeast from 1985 to 1987; excavations were still predominantly oriented towards the northeast and northwest quadrants in 1987. If directional orientation of excavations is related to thermal considerations, it would seem reasonable for excavations to be oriented towards cooler northern directions during summer months. It has been hypothesized that arctic foxes select favorable microclimate conditions in which to construct dens (Chesemore, 1969; Smits *et al.*, 1988). Red foxes on Assateague Island may also select microclimate conditions favorable for construction of fox dens.

Shrub succession and *Hudsonia* dune habitats were the two most important sites for red fox excavations on Assateague Island. These two habitats supported 96.2% of the total excavations in 1985 and 93.6% in 1987. Between 1985 and 1987 there was a significant increase in the use of *Hudsonia* dune habitat for red fox excavation location. Although this shift was significant, it probably does not constitute a major habitat change, since *Hudsonia* dune community usually occurs within the shrub succession habitat (Hill, 1984). In many places these two habitats merged together and one side of a dune was characterized by shrub succession habitat while the other side was predominantly *Hudsonia* dune habitat.

Between 1985 and 1987 the red fox population increased from an estimated eight breeding pairs to an estimated 11 breeding pairs. The average distance between centers of adjacent denning areas decreased from 3.4 km in 1985 to 2.6 km in 1987. This suggested that suitable red fox denning sites may not have been limited in 1985.

Red foxes have been reported to exhibit a universal preference for digging dens in sandy loam soils (Soper, 1942; Sheldon, 1950; Storm *et al.*, 1976; Pils and Martin, 1978) and well-drained soils (Scott and Selko, 1939; Layne and McKeon, 1956; Stanley, 1963). Sandy or loamy sand textured soils also appeared to be important factors influencing the location of fox excavations on Assateague Island. These two types of soils permit rapid water drainage and ease in digging excavations. They also were above the water table (Hall *et al.*, 1973), which may be an important factor in determining excavation location on Assateague. There was a significant increase in the use of sandy-textured soil for the location of fox excavations from 1985 to 1987. The sandy loam soil (klej) was restricted to an area west of the primary dunes from dune crossing 10 southward to approximately 1.0 km south of dune crossing

TABLE 4. Percent frequency of occurrence for prey items found in red fox scat on Assateague Island, Maryland. Results were based on the analysis of 56 scats found between May and August 1987.

| | PERCENT FREQUENCY |
|--------------------|-------------------|
| MAMMALS | 87.0 |
| Rabbit | 44.4 |
| Meadow Vole | 31.5 |
| White-footed Mouse | 24.1 |
| Unknown | 35.2 |
| CRUSTACEANS | 64.8 |
| BIRDS | 46.3 |
| PLANT | 42.6 |
| INSECTS | 31.5 |
| FISH | 9.3 |
| MOLLUSCS | 1.9 |
| UNKNOWN (Organic) | 37.0 |

11 (Fig. 1). Although the increase in the use of sandy-textured soil was statistically significant, it may not represent a major change in red fox preference. The change probably occurred due to a slight shift in the location of a denning area from 1985 to 1987. This shift moved the denning area location from the site where klej soil was restricted to an area just to the north.

Active dens are significantly different from both inactive dens and inactive pseudo-dens in the amount of open ground surrounding them. The large amount of barren ground associated with active dens may reflect the need for increased visibility while raising young. Less vegetation may also have resulted in higher wind velocities and thus fewer numbers of biting insects (Keiper and Berger, 1982) surrounding the excavations. Biting insects, which are abundant on Assateague, may influence red fox excavation location on Assateague Island.

Life expectancy of red fox excavations on Assateague was unknown, but due to constant sand shifting, it appeared that excavations in unprotected areas cover over within days or weeks. However, excavations in protected areas with shrub cover last several years. During the ground search in 1985, a researcher broke through the surface of a dune and discovered an old fox den, although no evidence of a den opening was present.

Although red fox food habits have been studied extensively in southern Wisconsin and Iowa (Errington, 1935, 1937), Michigan (Hamilton *et al.*, 1937), Maryland (Hockman and Chapman, 1983), Missouri (Korschgen, 1959), England (Southern and Watson, 1941), Ireland (Robertson and Whelan, 1987), central Alberta (Dekker, 1983), and Newfoundland (Dodds, 1955; Maccarone and Montevichi, 1981), studies on the food habits of red foxes on Atlantic barrier islands are apparently non-existent.

Red fox diets have been documented to consist largely of lagomorphs and rodents depending on their abundance (Errington, 1935; Scott, 1943; Wood, 1954; Dodds, 1955; Korschgen, 1959; Hockman and Chapman, 1983; Robertson and Whelan, 1987). Insects and fruit show seasonal fluctuations with the peak occurring

in summer and autumn (Ewer, 1973). *Microtus* appears to be an important food source for red fox in other regions of its distribution (Errington, 1935; Heit, 1944; Scott and Klimstra, 1955). Heit (1944) studied fox food habits in a salt marsh in Maryland and found *Microtus* to be the most frequent prey item in the scat, although the larger muskrat appeared to be the major food item in terms of total energy intake. Although muskrats were not found in the scat analysis, remains were found outside of red fox excavations. This suggests that muskrats were also consumed by red foxes on Assateague.

Dueser and Porter (1986) found that these species were common to abundant on Assateague Island during June - July 1978. Because this present study included analysis of only 56 red fox scats collected between May and August 1987, the results should not be viewed as representing the complete diet of red foxes on Assateague Island.

MANAGEMENT IMPLICATIONS

Fox den searches by fixed winged aircraft are not recommended for use on east coast barrier islands. Ground surveys, although manpower intensive, allowed us to readily locate fox excavations. Search activities may be expedited by scrutinizing sand dune habitats, since nearly all excavations were found in these areas. Information regarding red fox denning behaviors is important in developing management plans and protection of critical barrier island fox habitat.

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Biology of Large Grazing Mammals on the Virginia Barrier Islands

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The biology of three large grazing mammals has been studied on Assateague Island since 1975: the native white-tailed deer, the exotic sika deer and feral pony. Pony populations have more than doubled since 1975 (45-152 animals). Over a 12-year period, the foaling rate was 54.4% and foal survival was 88.3%. Mortality was estimated at about 5%. Ponies lived in discrete bands that do not defend territories. The number of bands and their size and composition changed over the course of the study. At low population levels in 1975, there were three harem bands with an average of 14 animals and 5.7 sexually mature mares per band. At the high population levels of 1988, there were 19 harem bands that averaged 5.7 animals and 2.7 sexually mature mares per band. Pony grazing over the years seems to have caused a gradual deterioration of the dune vegetation. This negative impact may increase in the future if the pony population continues to increase. The deer population appears to be composed of 75% sika and 25% white-tailed deer. For sika deer, males comprise 42.8% of the population, females make up 41.8%, and fawns total 15.4% of the population. For white-tail deer, the population is comprised of 52.4% males, 38.1% females, and 9.5% fawns. The average weight of 18 male sika deer was 22.25 kg, while 17 female deer averaged 19.39 kg. Ten sika fawns weighed an average of 10.86 kg. The number of white-tailed was too small for analysis. Fecal analysis in late autumn indicates little dietary overlap between deer and ponies but considerable overlap between white-tailed and sika deer.

Key words: white-tailed deer, sika deer, free-ranging ponies, large-mammal ecology

INTRODUCTION

Large grazing mammals are capable of causing serious habitat degradation, especially on oceanic islands. In the Galapagos Islands, feral mammals, particularly the goat, have destroyed the endemic tree cactus (Dawson, 1966). Goats have caused the disappearance of at least 48 indigenous and 18 introduced plant species on Santa Catalina Island (Thorne, 1967), and in Hawaii they have eliminated some species of plants and greatly altered the abundance and distribution of others (Yocum, 1967). The removal of vegetation by these animals has been so severe in some areas that extensive erosion has occurred along with an associated decrease in soil fertility and moisture retention (Coblentz, 1978).

Assateague Island, the largest of the Virginia barrier islands, supports populations of three large mammalian herbivores: the native white-tailed deer (*Odocoileus*

virginianus), the exotic sika deer (*Cervus nippon*), and feral pony (*Equus caballus*). Sika deer were introduced to the island in 1923 (Presnall, 1958); feral ponies most likely were released onto Assateague Island in the late 1600's by early Eastern Shore colonists.

To determine the effect of the large grazing Assateague Island, data have been collected since the biology of the white-tailed and sika deer and pony these data include information on the social characteristics of the population, and effects of mammals on the ecology of 1975 on various aspects of feral pony. For the feral organization, reproductive grazing on the dune vegetation. The data are less complete for the deer, but include information on the sex and age structures of the populations and food habits.

METHODS AND STUDY AREA

Assateague Island is a 61 km long barrier island located off the Atlantic coast of Maryland and Virginia. The Virginia portion of the island consists of approximately 3,680 hectares administered by the U. S. Fish and Wildlife Service as the Chincoteague National Wildlife Refuge. The Maryland portion of Assateague Island contains 3415 ha primarily administered by the National Park Service as the Assateague Island National Seashore.

Hill (1984) divided Assateague Island, Maryland, into eight vegetative communities on the basis of dominant plant species. His descriptions follow. These vegetative communities with the areal extents of each are salt marsh (1104.3 ha, 35.4% of the total area), shrub succession (476.1 ha, 15.3%), fresh water marsh (465.9 ha, 14.9%), non-vegetated (330.7 ha, 10.6%), dunegrass (311.5 ha, 10.0%), woodland (210 ha, 6.7%), *Hudsonia* dunes (140.6 ha, 4.5%), and washes and pans (80.9 ha, 2.6%).

The dunegrass community occupies elevated dunes (man-made or natural) which lie just west of the high tide mark. Little plant species diversity is present in this habitat which is dominated by American beachgrass (*Ammophila breviligulata*) and seaside goldenrod (*Solidago sempervirens*).

The shrub succession habitat is bounded on the east by the dunegrass community and on the west by a number of different communities. Few plant species are restricted to this habitat, which is characterized by the presence of black cherry (*Prunus serotina*), persimmon (*Diospyros virginiana*), chokeberry (*Pyrus angustifolia*), blackberries (*Rubus* spp.), poison ivy *Rhus radicans*), common greenbrier (*Smilax rotundifolia*), and bayberry (*Myrica* spp.).

The *Hudsonia* dune habitat usually occurs as habitat islands within the shrub succession. This community is defined by the presence of beach heath or poverty grass (*Hudsonia tomentosa*) but is also characterized by pinweeds (*Lechea maritima*), and sand jointweed (*Polygonella articulata*).

The woodland community is best described as a pine-deciduous woodland. The community occurs in isolated areas on stable dunes west of the shrub succession habitat, usually on the widest parts of the island (Hill, 1984). The dominant species in this community are loblolly pine (*Pinus taeda*), American holly (*Ilex opaca*), sassafras (*Sassafras albidum*), sweetgum (*Liquidambar styraciflua*), oaks (*Quercus* spp.), greenbriers (*Smilax* spp.), grapes (*Vitis* spp.), blueberries (*Vaccinium* spp.), and poison ivy.

Fresh water marshes are species-rich habitats found in transitional areas bordering the salt marsh and woodland communities (Hill, 1984). They are characterized by: salt marsh cordgrass (*Spartina alterniflora*), red maple (*Acer rubrum*), black willow (*Salix nigra*), bayberry, blueberries, cattails (*Typha* spp.), swamp rose (*Rosa palustris*), and common elder (*Sambucus canadensis*).

The salt marsh forms an extensive community dispersed throughout the entire length of the island. It is generally bounded on the east by either fresh water marshes or the woodland community, and on the west by the bay (Hill, 1984). The dominant plants in this habitat include salt marsh cordgrass, salt marsh hay (*Spartina patens*), slender glasswort (*Salicornia europaea*), sea lavender (*Limonium nashii*), spike grass (*Bistichlis spicata*), and marsh elder (*Iva frutescens*).

The washes and pans are mostly barren habitats and the plants they support are primarily succulent or fibrous halophytes. These include dwarf glasswort (*Salicornia bigelovii*), seabeach orach (*Atriplex arenaria*), low sea blite (*Suaeda linearis*), sand spurreys (*Spergularia* spp.), and large salt marsh aster (*Aster tenuifolius*).

Ponies

Since 1975, data were collected on the size, sex, and age composition of each of the bands living on the northern portion of Assateague Island (Keiper, 1976). Each pony living in the study area could be recognized individually by differences in color, sex, size, and markings. The birth date of each foal, its sex, and the age and identity of its mother were recorded each year (Keiper and Houpt, 1984).

Effects of pony grazing on the dune vegetation were studied using exclosures constructed in 1978. The exclosures were constructed on primary dunes, two near the northern tip of the island and eight at one mile intervals starting just south of Dune Crossing One. Each exclosure was 5 m² surrounded by a single strand of barbed wire strung tautly at a height of 78 cm above the ground. Ponies graze around the cages during the summer growth period. In late summer, 20 randomly selected 30 cm² samples of vegetation were cut from within and outside each cage. For sampling purposes, each cage and surrounding area was divided into four quadrants. Within each cage, one sample of ungrazed vegetation was obtained from each quadrat. Outside of the cage, two additional samples were removed from each quadrat from an area located within five meters of the perimeter of the cage. Two additional samples were removed from each quadrat in the area located between five and ten meters from the perimeter of each cage.

For each of the 20 samples removed per cage, all the vegetation within the 30 cm² sampling area was cut at ground level using hedge shears and collected in plastic bags. The bags were sent immediately to the laboratory at the Mont Alto Campus of the Pennsylvania State University. Each sample was oven-dried for one week at 45°C and weighed on a torsion balance (Eline and Keiper, 1979).

Deer

Deer sex, age and weight data were gathered from inspections of hunter-killed sika and white-tailed deer during the 1981 and 1982 hunting seasons. The check station was located at the island's sole land vehicle access point. Harvested deer were sexed, aged (tooth replacement and wear) and weighed (dressed weight). These data were compared to information collected by the National Park Service.

between 1978 and 1980 concerning the number of deer of each species killed by hunters.

Fifty pellet samples from known deer were collected from deer processed at the deer check station. Pellets were packed with table salt to dry them and prevent decomposition. Samples were sent to the Composition Analysis Laboratory at Colorado State University for analysis. Twenty microscope slides from each pellet sample were prepared and then the plant materials on the slides were compared to known plant reference slides.

RESULTS

Population Dynamics and Social Organization of the ponies

The pony population increased from approximately 45 animals in 1975 to 152 animals in 1988, an average increase of more than 8% per year. The size of the pony population during each year of the study is presented in Table 1.

Assateague ponies show a distinct seasonality of births. Foals are born from March to October with about half (52%) arriving in May. Eighty-eight percent of the foals are born in April, May, or June. Although the sex ratio of foals varies from year to year, over the course of the study the total number of colts (60) was almost equal the number of fillies (67).

The foaling rate (the percentage of sexually mature mares that foal each year) is low and variable, ranging from 40.9% to 70% with a 12-year mean of 54.4% (Table 2).

Survivorship of foals averaged 88.3%. Of the foals that died, 50% were colts indicating there was no differential mortality (Keiper and Houpt, 1984). Based on the number of ponies that disappear from the population and are never seen and cases of documented deaths, adult mortality was estimated at about 5% a year.

Effects of Pony Grazing

Results of the exclusion cage sampling are presented in Table 3. Data from the first year the cages were erected were compared with data collected in 1983 using a one-way analysis of variance with a randomized block design. For 1983 the experimental (*i.e.*, grazed) samples averaged less biomass than the control (*i.e.*, exclusion cage) samples. This difference was significant for samples taken within 5 m of the cage ($P < 0.05$) but was not significant for the samples taken in the area 5-10 m from the cage ($P > 0.05$). The reduced biomass outside of the exclusion cages may have resulted from increased grazing pressure related to the increased population size.

When the 1983 data were compared to those for 1978 (Eline and Keiper, 1979), no significant differences were noted between control samples ($P > 0.05$). The 1983 average control biomass was the same as that for 1978. Comparisons between 1978 and 1983 experimental samples show a decrease in biomass over the years outside the cages although only the difference between samples taken 5-10 m from the cage was statistically significant ($P < 0.05$).

Deer Sex, Age, and Weight

For the years 1978-1982, 260 deer were harvested on the Maryland portion of the Assateague Island National Seashore. Of this total, 200 deer (76.9%) were sika (Table 4), of which 42.8% were male, 41.8% were female, and 15.4% were fawns

TABLE 1. Age composition and population size of the pony population on Assateague Island National Seashore.

| Year | Males | Females | (1-2 yr.) | Foals | Total |
|------|-------|---------|-----------|-------|-------|
| 1975 | 6 | 18 | 11 | 10 | 45 |
| 1977 | 10 | 17 | 14 | 12 | 53 |
| 1979 | 11 | 22 | 20 | 9 | 62 |
| 1981 | 9 | 34 | 23 | 15 | 81 |
| 1983 | 17 | 44 | 18 | 23 | 102 |
| 1985 | 27 | 43 | 32 | 21 | 123 |
| 1988 | 38 | 58 | 28 | 27 | 152 |

TABLE 2. Foaling Rate (%) for Mares on Assateague Island National Seashore.

| Year | Sexually Mature Mares | Mares Foaling | Foaling Rate(%) |
|---------|--------------------------|---------------|-----------------|
| 1975 | 18 | 10 | 55.6 |
| 1976 | 14 | 9 | 64.3 |
| 1977 | 17 | 12 | 70.6 |
| 1978 | 20 | 14 | 70.0 |
| 1979 | 22 | 9 | 40.9 |
| 1980 | 30 | 17 | 56.7 |
| 1981 | 34 | 15 | 44.2 |
| 1982 | 35 | 18 | 51.4 |
| 1983 | 42 | 23 | 54.8 |
| 1984 | 39 | 19 | 48.7 |
| 1985 | 43 | 21 | 48.8 |
| 1988 | 58 | 27 | 46.6 |
| Average | | | 54.4% |

whose sex was not determined. Likewise, of 21 white-tailed deer harvested in 1981 and 1982, 11 (52.4%) were male, eight were female (38.1%), and two were fawns.

Other comparisons between the data collected in 1981 and the data recorded during the period 1978-1980 cannot be made because the deer harvested during the years 1978-1980 were not properly sexed or aged. Deer were classified as male and female apparently on the basis of the presence or absence of antlers. Male fawns would not show antlers, and could not be identified as male deer because the reproductive structures needed for proper sexual identification were destroyed by field dressing. Male fawns, therefore, were probably classified as female deer, effecting the validity of male:female sex ratios and preventing valid comparison with 1981 sex data.

Similarly because the data collected for the years 1978-80 did not distinguish between fawns and older animals and did not determine the ages of older deer, accurate information on the age structure of the population could not be gathered. The data on dressed weights for those years also did not differentiate between

TABLE 3. Comparison of the dry weight (g) of vegetation removed from 30-cm² samples within and outside of exclusion cages.

| Exclusion Cage | Control Samples Within Cage | | Samples Within 5 m Of Cage | | Samples 5-10 m From Cage | |
|-------------------|--------------------------------|------|-------------------------------|------|-----------------------------|------|
| | 1978 | 1983 | 1978 | 1983 | 1978 | 1983 |
| 1 | 15.3 | 27.8 | 16.5 | 22.7 | 18.9 | 15.9 |
| 2 | 11.7 | 14.0 | 14.5 | 11.9 | 15.8 | 14.4 |
| 3 | 20.9 | 34.0 | 19.0 | 12.4 | 23.9 | 19.8 |
| 4 | 17.5 | 15.8 | 15.7 | 13.0 | 17.7 | 13.0 |
| 5 | 17.8 | 13.0 | 17.9 | 14.6 | 16.5 | 11.8 |
| 6 | 22.7 | 19.6 | 20.6 | 12.1 | 19.6 | 17.6 |
| 7 | 11.6 | 19.4 | 6.7 | 9.5 | 13.5 | 9.8 |
| 8 | 30.5 | 12.8 | 31.6 | 14.5 | 41.4 | 16.2 |
| 9 | 20.1 | 15.4 | 20.5 | 11.2 | 23.3 | 13.1 |
| 10 | 22.6 | 18.7 | 14.8 | 8.7 | 20.1 | 10.9 |
| Average | 19.1 | 19.1 | 17.8 | 13.1 | 21.0 | 14.2 |

TABLE 4. Species composition of deer harvested on Assateague Island National Seashore, 1978-1982.

| Year | Sika Deer | White-Tailed | | % Sika Deer |
|-------|-----------|--------------|------------|-------------|
| | | Deer | Total Deer | |
| 1978 | 26 | 10 | 36 | 72.2 |
| 1979 | 38 | 13 | 51 | 74.5 |
| 1980 | 37 | 16 | 53 | 69.8 |
| 1981 | 52 | 11 | 63 | 82.5 |
| 1982 | 47 | 10 | 57 | 82.5 |
| Total | 200 | 60 | 260 | 76.9 |

weights of fawns and weights of adult animals so that the data cannot validly be compared with the weight data for known aged deer collected in 1981.

The male:female sex ratio approached 1.0 (1.03 for sika, 1.37 for white-tailed deer). Since the number of males and females are about equal at birth, these data suggest that mortality was not sex specific: hunters apparently do not selectively harvest male deer of either species. The relative percentage of sika deer in the total harvest has increased from 72% to 82% in the last five years.

The ages of 44 sika deer killed in 1981 were determined and of these 27 (61.4%) were fawns and yearlings. The average age of the sika deer tallied 2.02 ± 0.20 y ($\bar{x} \pm \text{SE}$). Females were more prevalent in the older age classes, but their average age ($\bar{x} = 2.75 \pm 0.37$ years) did not differ significantly ($P > 0.05$) from that of males ($\bar{x} = 2.2 \pm 0.21$ years). The fawn:adult female ratio, an indicator of reproductive

success, was 62.5%. These results suggest that the sika deer harvest was fairly heavy, with younger animals making up the principal kill. The harvest, in turn, appeared to be balanced by good reproductive success and rate of increase.

The age structure of the 11 white-tailed deer harvested in 1981 was similar to that of the sika deer, with five of the 11 being aged as fawns or yearlings. The remaining six deer were aged as three year olds. The small sample size precluded a more detailed analysis.

The dressed weights of 45 sika deer killed in 1981 were obtained. The mean weight of 10 sika fawns was 10.86 kg. Eighteen adult male deer averaged 22.25 kg, while 17 adult female sika deer averaged 19.39 kg. Two white-tailed deer fawns averaged 14.77 kg. Three male white-tailed adults averaged 39.23 kg. (the fourth male was not field dressed) while five female white-tails averaged 24.73 kg.

Deer Food Habits

Thirty-five categories of plants were identified in the fecal samples from sika deer and 23 from white-tailed deer (Table 5). Except for *Hudsonia tomentosa* (beach-heath), *Quercus* spp., and *Magnolia virginiana*, the composite of sika deer pellets contained the same plants ingested by the white-tailed deer. Only one white-tailed deer sample contained these genera. Browse species constituted 36% of the diet of white-tailed deer and 42% of the diet of sika deer.

Four genera of plants composed 90% of the relative density of the plant fragments in the sika deer pellets: *Solidago* spp. (golden-rod), which was present in all pellet samples and made up 34% of the relative density; *Myrica* spp. (wax-myrtle), found in 97% of the samples and composing 27% of the relative density; *Spartina* spp. (cordgrass), identified in 72% of the sika deer pellets and contributed 17% to the relative density; and *Rhus* spp. (dwarf sumac and poison-ivy), found in all of the sika samples and composing 13% of the relative density.

Four plant genera composed most of the late fall diets of white-tailed deer. These included: *Myrica* spp., found in 72% of the samples and composing 18% of the relative density; *Rhus* spp., identified in 94% of the white-tailed deer samples and composing 16% of the relative density; and *Solidago* spp., present in 89 of the samples and composing 15% of the relative density. pinweed (*Lechea maritima*) was found in all white-tailed deer samples and made up the greatest relative density (35%). Pinweed also was identified in 45% of the sika samples, but composed only 1% of the relative density. Conversely *Spartina* spp., an important plant in the sika's late fall diet, composed 0.14% of the relative density of plant fragments in white-tailed deer pellets and was identified in only one white-tailed deer sample.

Similarity of diets was examined using Spearman rank-correlation. plants were ranked in the order of their relative densities in the diet, then a correlation coefficient was calculated between the orders of abundance of the foods in the two diets. The rank-order correlation coefficients for foods eaten by white-tailed and sika deer were positively ($P < 0.02$) correlated.

DISCUSSION

Assateague ponies live in social groups called bands. The most common social unit is the harem band, which consists of one adult male, one to several adult females and their offspring, which are usually no more than three years of age. Other bands

TABLE 5. Plants consumed by deer on Assateague Island during late Fall 1982.

| Plant | white-tailed deer (n = 18) | | Sika deer (n = 29) | |
|----------------------------------|-------------------------------|---------------------------------|-----------------------|---------------------------------|
| | Frequency | % Relative density ^a | Frequency | % Relative density ^a |
| <i>Lechea maritima</i> | 100.0 | 34.73 | 44.8 | 1.25 |
| <i>Myrica</i> spp. (2 species) | 72.2 | 17.79 | 96.6 | 27.12 |
| <i>Rhus</i> spp. (2 species) | 94.4 | 16.42 | 100.0 | 13.19 |
| <i>Solidago</i> spp. (6 species) | 88.9 | 14.80 | 100.0 | 34.04 |
| Rosaceae type | 27.8 | 2.00 | 13.8 | 0.51 |
| <i>Rosa palustris</i> | 44.4 | 1.31 | 13.8 | 0.20 |
| Composite type | 11.1 | 0.87 | 3.4 | 0.10 |
| <i>Juniperus virginiana</i> | 22.2 | 0.77 | 13.8 | 0.46 |
| Fern | 22.2 | 0.76 | 34.5 | 1.08 |
| <i>Spartina</i> spp. (2 species) | 5.6 | 0.14 | 72.4 | 17.17 |
| <i>Distichlis spicata</i> | 0.0 | 0.00 | 34.5 | 1.42 |
| <i>Carex</i> spp. (3 species) | 0.0 | 0.00 | 24.1 | 0.38 |
| <i>Eleocharis albida</i> | 0.0 | 0.00 | 10.3 | 0.15 |
| <i>Panicum</i> spp. (12 species) | 0.0 | 0.00 | 13.8 | 0.15 |
| Other | | 10.41 ^b | | 2.78 ^c |

^aRelative density = (Density of fragments for a species/Sum of densities of fragments of all species)

x 100

^b9 genera

^c21 genera

include bachelor groups of two to four young males and mixed bands of young males and females. A few solitary ponies can be found.

The harem system of organization has been considered to be an adaptation to seasonally changing ecological conditions (Klingel, 1975). Because the stallion is non-territorial and defends his harem rather than a distinct territory, the group is not restricted in its movement and can wander about to make use of the best available food from season to season. Harem sizes range from two to 21 animals and average 3.4 to 12.3 individuals for a number of unmanaged populations with natural age and sex ratios (Table 6).

Apparently, the number of mares in a harem is related to the number of stallions in a population and to population density, so the number of harem bands and their size and composition on Assateague have changed over the course of the study. At low population levels in 1975 (45 ponies), there were only three harem bands with an average of 14 animals and 5.7 sexually mature mares per band. By 1984, when the pony population reached 110, 10 harem bands were present and averaged 9 ponies and 3.8 sexually mature mares per band.

With a population of 152 ponies in 1988, there were 19 harem bands that averaged only 5.7 animals and 2.7 sexually mature mares per band.

Harem bands are stable social units. Stallion tenure ranged from 0.01 to 4.2 years and averaged 2.11 years for 24 stallions in the Granite Range of Nevada (Besger, 1983); stallion tenure on Assateague Island, however, has lasted more than

TABLE 6. Feral horse harem band structure in North America.

| Population | Harem Size | | Mares Per Band | | No. of Bands |
|--|------------|---------|----------------|---------|--------------|
| | Mean | Maximum | Mean | Maximum | |
| Pryor Mountains, Wyoming (Feist and McCullough, 1975) | 5 | 9 | 1.8 | 3 | 44 |
| Toi Cape, Japan (Kaseda, 1981) | 6 | 13 | 1.5 | 3 | 13 |
| Sable Island, Canada (Welsh, 1975) | 5.5 | 20 | --- | --- | 47 |
| Grand Canyon (Berger, 1977) | 4.5 | 6 | 3 | 4 | 4 |
| Assateague Island (low population density) | 14 | 18 | 57 | 6 | 3 |
| Assateague Island (high population density) | 5.7 | 12 | 27 | 7 | 19 |

10 years. The composition of adult mares in a harem band also is stable, with some mares remaining in the same band for life (Keiper, 1985).

Most of the changes in harem band membership resulted from the emigration and immigration of subadult animals. Generally, both colts and fillies leave their natal bands for other groups, although on Assateague Island approximately 25% of young females never dispersed and were bred by their fathers (Keiper and Houpt, 1984).

Dispersing fillies are integrated into existing harems or start a new family with a bachelor male. Others remained alone for more than a year (Keiper, 1985). Dispersal occurs primarily before the age of 2 years and may reflect the onset of sexual maturity. Those fillies who depart usually wander away without the stallion's intervention. However, some are chased away by adult mares.

Most young stallions dispersed between 12-24 months of age, wandering off with a sibling or by themselves (Keiper, 1985). In the Red Desert of Wyoming, young males were reported to leave their natal band on their own accord (Denniston, 1979), but on Assateague Island, they were usually forced to disperse by aggressive harassment by the harem stallion (Keiper, 1985). Bachelor males become harem stallions by abducting a mare from a harem band, joining mares whose stallion has died, joining with a dispersing young female, or ousting a harem stallion. Multi-male bands result when more than one bachelor joins a mare or family unit, when a young stallion stays in his natal band after reaching maturity, or when several young male and female horses disperse from the same harem band and remain together until they become sexually mature (Keiper, 1985).

The seasonality of births shown by the Assateague ponies is consistent with other studies of free-ranging horses. Feist and McCullough (1975) reported foaling between April 15 and June 30. Of 294 births in New Forest ponies, 96% occurred from April to June (Tyler, 1972). In Sable Island ponies, foals were born in all months but January. However, almost 77% were born in April, May or June, and only 5.6% of all foals were born between October and February (Welsh, 1975). With

respect to sex ratio, Tyler (1972) reported that 54.5% of all foals born in the New Forest were female. On Sable Island, female foals made up 51% of all foals born from 1970 to 1972 (Welsh, 1975).

Over a 12-year period, the percentage of sexually mature mares that foaled each year was 54.4%. This figure is comparable with the 59.6% foaling rate for mares on Sable Island, Canada (Welsh, 1975). Tyler presented a three-year foaling rate of 46% for the New Forest ponies in England.

The fluctuation in the foaling rate from one population to another and from one year to the next is probably the result of the age structure of the breeding population. Young mares begin to foal as early as three years, but foal at a lower rate than older mares. For western mustangs the percentage of females that foaled was only 13% for 3-year-olds compared with 66% for females 5 years old and older (McCort, 1984). Similarly, on Assateague Island the foaling rate for 3-year-olds was only 23%. For 4-year-olds, the rate was 46%, whereas for 5-year-olds the rate increased to 53% (Keiper and Houpt, 1984).

As the percentage of young mares in the population changed, fluctuations in the foaling rate occurred. For example, in 1977, when the foaling rate was 70.6%, the northern Assateague population consisted of 17 sexually mature mares. Fourteen of the mares were over 5 years, whereas only 3 of the mares were 5 years old or younger. On the other hand, in 1980 and 1981, mares 3 and 4 years old made up over 40% of the breeding population and the foaling rates were only 56.7% and 44.2% for those years (Keiper and Houpt, 1984).

The exclusion cage results suggest that the condition of the vegetation on the primary dune in the study area would not have changed greatly between 1978-1983 if ponies had not been grazing the dunes. Pony grazing over the years seems to have caused a gradual deterioration of the dune vegetation and this negative impact may increase over the years as the pony population increases. The difference in vegetation outside of and within the exclusion cages may also have been effected by the wind depositing excess sand on top of existing vegetation or eroding sand from beneath the plants.

Examination of the data on hunter-killed deer suggest that sika deer have been increasing in abundance on Assateague, perhaps at the expense of white-tailed deer. In several other areas following introduction, sika deer have out competed sympatric species of deer. This has been noted for populations of red deer (*Cervus elaphus*) in New Zealand (Kiddie, 1962) and this may be occurring for sika and white-tailed deer in Dorchester County, Maryland (Feldhamer and Chapman 1978). The success of the sika deer may be attributed to their more diverse and adjustable feeding habits as opposed to any overtly aggressive behavioral traits (Feldhamer and Chapman, 1978). It may also be possible that white-tails are affected by differential hunting pressure, either because they are more easily seen or simply preferred by hunters because they yield more meat. In an attempt to diminish or reverse white-tail decline, the National Park Service has closed the hunting season for white-tails, and increased the bag limit for sika deer to three animals.

Although the late fall diets of white-tailed and sika deer appear similar, the actual degree of dietary overlap and possible competition is unclear. because plant fragments were identified only to the genus level. In groups where 1 species per

genera were present (like for *Rhus*, *Myrica*, and *Solidago*), the deer could have been foraging on different species.

Sika deer forage on a greater variety of plants than white-tailed deer. I attribute this observation to sika deer apparently feeding more in the fresh and salt marshes, as evidenced by plants like *Spartina* spp., *Carex* spp., *Distichlis spicata* (seashore saltgrass), and *Eleocharis albidia* (spikerush) in the sika composite.

Sika deer seem to be well established on Assateague Island. They appear to have more diverse food habits, at least in late fall, and are better competitors in over-browsed habitats (Feldhamer and Chapman 1978), a condition that may occur on Assateague Island as deer populations increase.

Grasses were relatively unimportant in the deer diet, meaning there was little overlap in the diet between deer and ponies and hence little feeding competition in late autumn. Deer feeding also apparently has little impact on dune vegetation.

Since diet usually changes from season to season, diet overlap and hence feeding competition may occur between deer or deer and ponies, especially in late winter when food supply is limited. Dietary studies, therefore, should be extended to other seasons of the year before definite conclusions are drawn.

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Herpetofauna of the Virginia Barrier Islands

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ABSTRACT

Twenty-nine species of amphibians and reptiles have been recorded from the Virginia Barrier Islands, compared with 46 species from mainland Eastern Shore. Assateague, Chincoteague, Parramore, Hog, and Smith Islands have the highest species diversity, apparently because of a greater variety of vegetative habitats and presence of freshwater. Knowledge of the herpetology of these islands is still in the exploration stage; several islands have yet to be surveyed. A brief history of herpetological exploration and observations on the known biology of each species are presented. Particular attention is paid to the species' insular ecology. Forty-two percent of the mainland amphibian fauna is represented on the islands, compared to 78% of the reptilian fauna. Examination of models of island formation suggests that it may not be necessary to invoke dispersal over saltwater to explain the origin of the island herpetofaunas. The linear relationship of species number to island area is positive and significant, whereas the relationship of species number to isolation from the mainland is nonsignificant. Elimination of Assateague Island from the analysis, because of the presence of man-altered habitats, renders the species-area relationship nonsignificant.

Key words: amphibians, reptiles, insular ecology, biogeography

INTRODUCTION

The amphibian and reptile fauna of the Virginia barrier islands is a subset of species derived from the Delmarva herpetofaunal assemblage. We present a brief history of herpetofaunal exploration, an annotated checklist, and a discussion of

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the biogeography of this fauna. Basic research is still needed on both the mainland Eastern Shore and the barrier islands, however, before the checklists can be considered complete. Little ecological research has been done on the amphibians and reptiles of the barrier islands. This decreases our ability to evaluate the origins of biogeographical patterns. Thus, the chief purpose of this paper is to provide a basis for future herpetological research in the region.

HERPETOFAUNAL EXPLORATION

C. W. Richmond obtained *Bufo woodhousii*, *Coluber constrictor*, *Elaphe obsoleta*, and *Nerodia sipedon* on Smith Island on 16 May 1894, the earliest collection date known. In the summer of 1899, Perry Schufelt collected *Sceloporus undulatus* and *Scincella lateralis* from Smith Island, Paul Bartsh took an *Opheodrys aestivus* on Smith Island in June 1897, and E. A. Mearns obtained a series of *Bufo woodhousii fowleri* from Smith Island in May 1910. On 4-7 May 1912, H. W. Fowler visited Assateague, Chincoteague, and Wallops Islands, and published the first notes on their herpetofauna (Fowler, 1925). In the same journal, M. K. Brady (1925) reported on ten species he found on Hog Island during June 1925. A single page of notes found in the "unknown" file in the Division of Amphibians and Reptiles, National Museum of Natural History, dated "17-20 June" (no year), was apparently authored by Brady. These notes indicate he also visited Cobb and Pig Islands (Pig Island was then a grass-covered low dune connected to Cobb Island in shallow water; it no longer exists). A single specimen of *Opheodrys aestivus* was collected by C. C. Sperry on Cobb Island on 26 June 1924 for the U.S. Biological Survey.

Conant first visited the islands 28-29 April 1947, when he obtained several species on Parramore and Hog Islands and made extensive collections on the adjacent mainland. His interest in the Virginia barrier islands stemmed from his intensive fieldwork on the herpetofauna of the Delmarva Peninsula, on which he briefly reported in 1945. His collections made between 1936 and 1948 and in 1957 and 1975 helped to provide much of the basis for our understanding of the composition of the herpetofauna of this region. The first general published list of amphibians and reptiles of the Virginia barrier islands was provided by Conant in 1981.

Over a period of several years (1950-1973) single specimens of a variety of species were donated to the U.S. National Museum of Natural History by people who visited Assateague and Chincoteague Islands. Lee (1972, 1973) summarized his observations on the herpetofauna of Assateague Island made during 1968-1972. A U.S. Fish and Wildlife Service team headed by R. B. Bury explored Parramore and Smith Islands during four weekend periods in November 1974, October 1975, and April and June 1976.

Recent herpetological research stems from three sources. Scott (1986) reported on sexual dimorphism, variation, and seasonal activity in a population of hognose snakes (*Heterodon platirhinos*) on Assateague Island. Dunson (1970, 1985, 1986) compared salinity tolerances and studied growth and physiology of five freshwater turtles and one estuarine turtle. Mitchell and Pague visited seven islands (Assateague, Chincoteague, Wallops, Parramore, Hog, Cobb, and Smith) during 22-30 May 1986. They also visited Cobb and Hog Islands on 11-12 June 1987. Their objectives were to obtain voucher specimens for species and islands lacking them,

and to gain some insight into the biogeography of the herpetofauna of this near-shore archipelago. They also began a mark-recapture study of the snakes of Cobb Island during this time. Pague visited five islands on 20-22 September 1988. Barry Truitt, current manager of the Virginia Coast Reserve, provided additional records for Myrtle Island in 1985 and 1986.

SPECIES ACCOUNTS

The mainland Eastern Shore of Virginia harbors 46 species of amphibians and reptiles (Mitchell and Pague, in press). Eight species of amphibians and 21 species of reptiles have been recorded from the Virginia barrier islands (Table 1). Of these, ten species have been found only on Assateague, Chincoteague, and Wallops Islands (7 amphibians and 3 reptiles). The following notes are included to summarize what we know about the distribution and ecology of each species on the islands, and to indicate where further research is needed. Comments about freshwater were derived from the literature, G.J. Hennessey and B. Truitt (pers. comm.), and our own observations. Explanation of museum designations are in Acknowledgments. USNMFH and CMFS indicate specimens with USNM or CM field tag numbers. TNC records refer to notes housed in the Virginia Coast Reserve at Brownsville and VIMS records are those housed in the Virginia Institute of Marine Science in Gloucester Point, Virginia. Common names follow Collins *et al.* (1982)

Plethodon cinereus (Green)

The redback salamander is the only salamander found on the Virginia barrier islands. J.C. Bridwell obtained two specimens on Chincoteague on 22 September 1938 (USNM). Conant collected five individuals under rotting pine logs on Chincoteague Island on 11 April 1941 (CM) within 30 m of where a small attenuated marine estuary extended into the island. This species has also been found on barrier islands in Georgia and South Carolina (Gibbons and Coker, 1978).

Bufo woodhousii fowleri Hinckley

Fowler's toads have been reported from five islands (Table 1; ANSP, GMU, USNM), all of which have, or have had, freshwater or weak brackish water. It is currently the only amphibian known from a Virginia barrier island other than Assateague, Chincoteague, or Wallops. The presence of viable populations presumably depends on freshwater for development of eggs and larvae. Brady (1925) and Scott (1986) found breeding adults and larvae in freshwater ponds, whereas Lee (1972) reported a breeding congregation in a slightly brackish pool. Adults can tolerate dry terrestrial environments and at least temporary exposure to saltwater; Engles (1952) noted that this toad entered saltwater when pursued. Brady (1925) reported that toads on Hog Island preyed upon the land amphipod *Orchestia gryllus*.

Bufo woodhousii was recorded as being abundant by Brady (1925), Lee (1972), and Scott (1986). Neither Conant, during the 1940's, nor the U.S. Fish and Wildlife Service team in the mid-1970's found this species on Hog, Parramore, or Smith Islands where it had been observed previously. Mitchell and Pague have since (1986) seen these toads on Smith Island and B. Truitt (pers. comm.) reports them common there. Toad populations may be adversely affected by coastal storms that add salt to freshwater ponds and pools. The freshwater ponds seen by Brady (1925)

Table 1. Amphibians and reptiles of the Virginia barrier islands. Records represented by voucher specimens are indicated with an "X", unvouchered observations and literature records with an "O", and a questionable record is indicated with a "?". Assateague (AS), Chincoteague (CH), Wallops (WA), Parramore (PA), Revel (RE), Hog (HO), Cobb (CO), Wreck (WR), Myrtle (MY), Smith (SM), Fisherman (FI).

| Species | Barrier Island | | | | | | | | | | |
|-------------------------------|----------------|----|----|----|----|----|----|----|----|----|----|
| | AS | CH | WA | PA | RE | HO | CO | WR | MY | SM | FI |
| Salamanders | | | | | | | | | | | |
| <i>Plethodon cinereus</i> | | X | | | | | | | | | |
| Anurans | | | | | | | | | | | |
| <i>Bufo woodhousii</i> | X | X | X | | | X | | | | X | |
| <i>Hyla cinerea</i> | O | X | | | | | | | | | |
| <i>Pseudacris triseriata</i> | O | | | | | | | | | | |
| <i>Rana catesbeiana</i> | X | | | | | | | | | | |
| <i>Rana clamitans</i> | X | | | | | | | | | | |
| <i>Rana palustris</i> | | | X | | | | | | | | |
| <i>Rana utricularia</i> | X | X | O | | | | | | | | |
| Turtles | | | | | | | | | | | |
| <i>Caretta caretta</i> | O | | | O | | O | O | O | | O | O |
| <i>Chelonia mydas</i> | O | | | O | | O | | | | | |
| <i>Chelydra serpentina</i> | O | O | O | X | | O | | | | X | |
| <i>Chrysemys picta</i> | O | O | | | | | | | | | |
| <i>Clemmys guttata</i> | O | O | | | | X | | | | X | |
| <i>Dermochelys coriacea</i> | O | | | O | | | | O | | O | |
| <i>Kinosternon subrubrum</i> | X | O | O | X | | X | | | | X | |
| <i>Lepidochelys kempi</i> | | | | | | O | | | | | O |
| <i>Malaclemys terrapin</i> | X | X | O | X | O | X | O | | O | X | X |
| <i>Pseudemys rubriventris</i> | O | | | | | | | | | | |
| <i>Terrapene carolina</i> | O | | | | | | | | | X | O |
| Lizards | | | | | | | | | | | |
| <i>Sceloporus undulatus</i> | O | | | | | | | | | X | |
| <i>Scincella lateralis</i> | | | | | | | | | | X | X |
| Snakes | | | | | | | | | | | |
| <i>Coluber constrictor</i> | X | O | X | | | O | | | | X | |
| <i>Diadophis punctatus</i> | | X | | | | | | | | | |
| <i>Elaphe obsoleta</i> | X | | O | | | O | O | | | O | |
| <i>Heterodon platirhinos</i> | X | X | O | | | O | | | | | |
| <i>Lampropeltis getula</i> | | | | | | | | | | X | |
| <i>Nerodia sipedon</i> | X | O | O | X | | O | | | | X | |
| <i>Opheodrys aestivus</i> | X | | O | X | O | X | X | X | X | X | X |
| <i>Storeria dekayi</i> | | | | X | | X | X | | | | |
| <i>Virginia valeriae</i> | | | | | | | ? | | | | |

on Hog Island have been long since displaced seaward by island erosion and movement (Conant, pers. obs.; B. Truitt, pers. comm.).

Hyla cinerea (Schneider)

The green treefrog is apparently common on Assateague Island (Lee, 1972). Mitchell and Pague collected this species on Chincoteague Island on 29 May 1986 (USNM). Populations of green treefrogs are known to occur in brackish marshes

(Neill, 1958). Gibbons and Coker (1978) listed this frog from nearly every island they tabulated along the coast of the southeastern United States.

Pseudacris triseriata kalmi Harper

The New Jersey chorus frog was reported from Assateague Island by Lee (1973), who heard large choruses at the southern end of the island in the early part of that year. Gibbons and Coker (1978) listed no member of the *triseriata* complex of *Pseudacris* from any barrier island.

Rana catesbeiana Shaw

Bullfrog tadpoles were collected in a shallow, drying impoundment by CAP and JCM on Assateague Island on 29 May 1986 (USNMFH). This species was recently documented from Bodie Island, North Carolina (Braswell, 1988). It has not been reported from other barrier islands studied (Gibbons and Coker, 1978; Gibbons and Harrison, 1981).

Rana clamitans melanota (Rafinesque)

Five green frogs were collected on Assateague Island on 20 October 1984 by C.H. Ernst and S. W. Gotte (GMU). This species (*R. clamitans*) has not been recorded from any other barrier island along the Atlantic seaboard (Gibbons and Coker, 1978). It is common on the mainland Eastern Shore.

Rana palustris Le Conte

A single pickerel frog was collected on Wallops Island on 20 October 1984 by C.H. Ernst and S.W. Gotte (GMU). Pickerel frogs have not been recorded from any other coastal island (Gibbons and Coker, 1978). The closest known locality is in Worcester County, Maryland (Harris, 1975).

Rana utricularia Cope

Lee (1972) found adult southern leopard frogs behind the primary dunes at the southern end of Assateague Island. Voucher specimens are known for Assateague (USNM) and Chincoteague (ANSP, CM, UMMZ, USNM) Islands, and W.A. Dunson observed it on Wallops Island. This frog is frequently found in brackish marshes (Neill, 1958), and has been recorded on many of the southeastern coastal islands (Gibbons and Coker, 1978).

Caretta caretta (Linnaeus)

Loggerhead sea turtles are commonly seen in the estuarine channels, and stranded individuals have been observed on the beaches of Assateague (VIMS), Parramore (TNC), Hog (VIMS), Cobb (VIMS), Wallops (TNC), Wreck (TNC), Smith (TNC, VIMS), and Fisherman (VIMS) Islands. Lee (1972) reported a nesting female on Assateague Island in 1972. A headstart program (relocation and captive incubation of nests) started by the U.S. Fish and Wildlife Service in 1969 on Assateague Island (Lee, 1972) was apparently unsuccessful. One female was observed nesting on the north end of Parramore Island on 18 June 1979 (B. Truitt, pers. comm.). Brady (1925) noted that large numbers were caught on hook and line and in nets around Hog Island. Lutcavage and Musick (1985) reported aggregations of loggerheads on the Atlantic side of the barrier islands. We assume that turtles seen in the estuary are utilizing the area for feeding. They prey primarily on horseshoe crabs (Keinath *et al.*, 1987).

Chelonia mydas mydas (Linnaeus)

Brady (1925) found a stranded Atlantic green turtle on Hog Island and VIMS has a record for Parramore Island. Schwartz (1960) recorded a female in Chin-

Table 2. Diversity and biomass of turtles in two unnamed mainland tidal creeks near Chincoteague (see Dunson, 1986) and a freshwater impoundment on Assateague Island, Virginia. Values are biomass in kg; number of individuals in parentheses. All data are from W. A. Dunson (pers. comm.)

| Species | Creek A | Creek C | Assateague |
|----------------------|-----------|------------|-------------|
| <i>C. serpentina</i> | 22.46 (8) | 85.74 (36) | 102.60 (24) |
| <i>K. subrubrum</i> | 0.14 (1) | 1.28 (12) | --- |
| <i>C. guttata</i> | 0.44 (3) | 1.30 (10) | --- |
| <i>M. terrapin</i> | 9.75(11) | 0.76(1) | --- |

* Occurred commonly but not quantified; several *Chrysemys picta* also caught.

coteague Bay at White Rock, Worcester County, Maryland. Green turtles are carnivorous as juveniles and feed almost exclusively on submerged sea grass as adults (Musick, 1979).

Chelydra serpentina serpentina (Linnaeus)

The common snapping turtle has been found on six islands: Assateague (Lee, 1972; Dunson, 1986), Chincoteague (Fowler, 1925), Wallops (W.A. Dunson, pers. comm.), Parramore (AMNH), Hog (Brady, 1925), and Smith (USNM). It is known from only four other Atlantic barrier islands (Gibbons and Coker, 1978). All observations were of turtles in freshwater ponds or pools. W.A. Dunson (pers. comm.) found that a population of this species in a freshwater impoundment on Assateague Island was comprised of 7 immatures, 6 females, and 11 males. Total biomass for this population was higher than that found for either of two mainland tidal creeks (Table 2). *Chelydra serpentina* commonly utilizes tidal habitats on the Eastern Shore of Virginia (Dunson, 1986). We conclude from his work that adults could easily colonize barrier islands.

Chrysemys picta picta (Schneider)

Lee (1972) found the eastern painted turtle to be moderately common in freshwater impoundments on Assateague Island and Fowler (1925) reported it from Chincoteague. It is abundant in freshwater habitats on mainland Eastern Shore but is unrecorded from other coastal islands. It was most likely introduced on Assateague, and a Chincoteague resident claims to have done so (W.A. Dunson, pers. comm.).

Clemmys guttata (Schneider)

Spotted turtles have been found on Hog and Smith Islands (USNM) and observed on Assateague (Lee, 1972) and Chincoteague (Fowler, 1925). The U.S. Fish and Wildlife Service team found six individuals on 23 October 1975 in small freshwater pools in the mixed pine-hardwood forest on Smith Island. Average carapace length of five specimens from the islands (96.9 mm, 92.3- 100.7) was nonsignificantly smaller than that of eight specimens from mainland Eastern Shore (106.9 mm, 84.5-120.0) ($t = -1.84$, $P = 0.094$). Spotted turtle biomass was nearly equal to that of mud turtles in two mainland tidal creeks (Table 2).

W.A. Dunson (pers. comm.) found spotted turtles in tidal water of no more than 6% normal seastrength at high tide in a mainland creek. Growth in adults occurred in water up to 36.2% seastrength (Dunson, 1986), however, within the range of

values he reported for *C. serpentina*. Adults are therefore likely to be able to tolerate seawater for limited periods of time, although they are less likely than snapping turtles and mud turtles to disperse from the mainland to the islands.

Dermochelys coriacea (Linnaeus)

The leatherback sea turtle is the rarest of the sea turtles recorded from the barrier islands. It is normally seen only several miles offshore and in the mouth of Chesapeake Bay (B. Truitt, pers. comm.). One was reported stranded on Parramore Island on 21 June 1938 by F.M. Uhler (photo available in Conant's files). G.J. Hennessey (pers. comm.) reported that George Reiger saw an enormous leatherback seven miles east of Wachapreague Inlet on 26 July 1980. VIMS has records for Assateague, Wreck, and Smith Islands. Leatherbacks are pelagic and feed primarily on jellyfish (Musick, 1979).

Kinosternon subrubrum subrubrum (Lacépède)

Eastern mud turtles have been observed on Chincoteague and Wallops Islands (Fowler, 1925; W.A. Dunson, pers. comm.) and collected from Assateague (USNM), Parramore (CM), Hog (USNM), and Smith (USNM) Islands. Brady (1925) found them to be abundant in freshwater ponds on Hog Island but the reduction of freshwater habitat on this island has probably reduced the mud turtle population. Carapace lengths of 14 adult museum specimens from the islands (males: 69.5-90.0 mm, $\bar{X} = 81.0 \pm 7.2$, $n = 7$; females: 73.3-100.0 mm, $\bar{X} = 80.4 \pm 9.1$, $n = 7$) average smaller than that of a sample we obtained from a pond above a mainland tidal creek near Oyster (males: 82.2-107.7 mm, $\bar{X} = 96.8 \pm 6.9$, $n = 11$; females: 82.1-89.7 mm, $\bar{X} = 85.6 \pm 2.6$, $n = 6$). The difference between males is significant ($t = -4.64$, $P < 0.001$). Mean body mass of mud turtles in a tidal creek population near Chincoteague (106.7 g, Table 2) was substantially lower than mean body mass of adult turtles from the freshwater pond population near Oyster (149.3 g).

W.A. Dunson (pers. comm.) found *K. subrubrum* in mainland tidal creeks that experienced salinities of 6-51‰ normal seastrength at high tide. Growth in hatching mud turtles from tidal creeks occurred up to a salinity of 45‰ seastrength (Dunson, 1986), higher than the values he observed for *C. serpentina*. The occurrence of this species on the barrier islands probably depends on the availability of fresh to brackish water. Conant found mud turtles in freshwater, but much more frequently in brackish water habitats on the Delmarva peninsula.

Lepidochelys kempi (Garman)

The Atlantic ridley sea turtle is rarely seen among the barrier islands (B. Truitt, pers. comm.). G.J. Hennessey found and carefully examined a small ridley (straight-line carapace length 35.6 cm) found dead at the south end of Hog Island on 14 September 1980. He also observed a slightly larger turtle that appeared to be a ridley on 25 June 1980 "inside a temporal inlet in mid-Metomkin Island in very shallow water." VIMS has a record for Fisherman Island. Some individuals may use the barrier island estuary as a feeding ground; they specialize on blue crabs (Lutcavage and Musick, 1985). This estuary is apparently not as important to immature ridleys as the Chesapeake Bay (Lutcavage and Musick, 1985; Keinath, *et al.*, 1987).

Malaclemys terrapin terrapin (Schoepff)

The northern diamondback terrapin occurs on all of the Virginia barrier islands. Vouchered records exist for Assateague (CM), Chincoteague (UMMZ), Parramore (CM, GMU, USNM), Hog (GMU, MSB, USNM), Smith (GMU, MCZ, USNM), and Fisherman (VCU) Islands, and unvouchered records exist for Revel (B. Truitt, pers. comm.), Cobb (TNC records), Wreck (TNC records), and Myrtle (B. Truitt, pers. comm.) Islands. It is the only truly estuarine representative of the herpetofauna and is the most commonly seen reptile on and around the islands, especially in late-spring and summer. Neill (1958) found no records of this species in freshwater. It is abundant in the marshes between the mainland and the islands. Other authors (e.g., Brady, 1925; Lee, 1972) noted the abundance of this species on the barrier islands and in the estuary. This turtle was hunted extensively between 1880 and 1930 for the restaurant trade, but the market declined in the 1930's (Conant, 1955; Ernst and Barbour, 1972). A recent upsurge in the restaurant trade was documented by Garber (1988), who noted that some turtles were caught in Virginia, probably near the town of Chincoteague (B. Truitt, pers. comm.). The harvest rates are unknown and we do not know what the impact on natural populations will be.

Females lay an average of 11.2 eggs per clutch from 30 May and to about 25 July in open sandy areas away from vegetation above the high tide line. Females may lay more than one clutch per season. Maximum carapace length of females recorded for the islands is 205 mm and for males is 143 mm, indicating strong sexual dimorphism. Dunson (1970, 1985) and Robinson and Dunson (1976) studied growth and physiology of hatchlings in relation to salinity tolerances. Diamondback terrapins specialize on molluscan prey.

Pseudemys rubriventris rubriventris (Le Conte)

Lee (1972) observed the redbelly turtle in man-made freshwater impoundments on Assateague Island. Although it is abundant on mainland Eastern Shore (JCM and CAP, unpublished), it is scarce on Assateague (W.A. Dunson, pers. comm.) and has not been reported from any other island. We have found adult specimens of this species in the Chesapeake Bay encrusted with barnacles (JCM and CAP, unpublished), suggesting some tolerance of salt water.

Terrapene carolina carolina (Linnaeus)

Lee (1973) reported seeing an eastern box turtle on Assateague Island. The U.S. Fish and Wildlife Service team found five adults in pine hardwoods on Smith Island (USNM) on 23 October 1975 and Mitchell and Pague found one adult female under grass cover on Smith Island on 23 May 1986. G.J. Hennessey received information about a shell found on Fisherman Island in 1976, but since US Route 13 crosses this island, the possibility of an intentional release cannot be ruled out. Box turtles can withstand difficult weather conditions by withdrawing into their shells and resting in ground forms and under grass clumps. Fresh water is apparently necessary for populations in Virginia (JCM and CAP, pers. obs.); it is not known how much metabolic water is obtained from the fruits, berries, and animal prey they eat. Latham (1916) found box turtles in salt water on Long Island. Box turtles are known to occur on only one other barrier island, Kiawah Island, South Carolina (Gibbons and Harrison, 1981). They may have been brought to Smith Island by former human inhabitants.

Sceloporus undulatus hyacinthinus (Green)

Lee (1972) reported that two adult northern fence lizards were observed in a loblolly pine stand on the southern end of Assateague Island. Two adult females were collected by Percy Schufeldt in the summer of 1899 from Smith Island (USNM). The ecology of this species on the islands is unknown. This species also occurs on Cumberland Island, Georgia (Gibbons and Coker, 1978).

Scincella lateralis (Say)

The ground skink has been confirmed from Smith (MSB, USNM) and Fisherman (VCU) Islands. This skink has been reported from barrier islands in North Carolina and South Carolina (Gibbons and Coker, 1978). Conant collected two and observed four others on Smith Island on 20 October 1948; they were under boards and the bark of a decaying log. Mitchell and Pague found one in a supratidal grassy area of Smith Island on 28 May 1986. Neill (1958) noted that this skink avoids areas that are damp from salt spray. Little is known of its ecology on the barrier islands. We suspect that juveniles of *C. constrictor* may prey upon these skinks.

Coluber constrictor constrictor Linnaeus

The northern black racer has been recorded from Assateague (AMNH, USNM), Chincoteague (W.A. Dunson, pers. comm.), Wallops (CMFH), Hog (Brady, 1925; TNC records), and Smith (USNM) Islands. It has been found on all the Atlantic barrier islands listed by Gibbons and Coker (1978). Brady (1925) noted they were seen in the tops of myrtle trees and those that were pursued on the ground sought protection in the myrtles. Both Brady (1925, Hog) and Lee (1972, Assateague) reported them to be uncommon. Mitchell and Pague, however, found this snake to be the most abundant terrestrial reptile on Smith Island on 28 May 1986. The catholic nature of this snake's diet and its ability to inhabit xeric habitats (JCM and CAP, unpublished) allow it to flourish on barrier islands.

Diadophis punctatus edwardsii (Merrem)

A single northern ringneck snake was collected by J.C. Bridwell at Chincoteague on 26 September 1938 (USNM). This is the only record for any barrier island along the Atlantic Seaboard (see Gibbons and Coker, 1978).

Elaphe obsoleta obsoleta (Say)

The black rat snake has been collected from Assateague (USNM) and Wallops (JCM photo) Islands and has been observed on Hog, Cobb, and Smith Islands (TNC records). This species has been reported for all but one Atlantic barrier island previously studied (Gibbons and Coker, 1978). It is an uncommon species on the islands but abundant on mainland Eastern Shore (RC, JCM and CAP, pers. obs.). On 23 June 1978, B. Truitt and B. Williams observed an adult individual that appeared to have washed up on the beach of Cobb Island. The snake was alive but appeared emaciated. We are unaware of a population on Cobb Island. Black rat snakes prey primarily on small rodents and birds (Uhler *et al.*, 1939; JCM and CAP, unpublished). The occurrence of these snakes on some of the barrier islands may be limited by the availability of prey populations.

Heterodon platirhinos Latreille

The eastern hognose snake has been verified from Assateague (USNM) and Chincoteague (USNM) Islands and observed on Wallops (Fowler, 1925) and Hog (Brady, 1925) Islands. Brady (1925) noted they were abundant on Hog Island, but extensive recent field work revealed none (R. Dueser, RC, JCM, and CAP, pers.

obs.). Minimum population density was estimated to be 4.8 snakes/ha on the southern end of Assateague Island (Scott, 1986). The presence of this species may depend on the occurrence of its primary prey, Fowler's toads. The decline of the hognose snake population may have followed that of the toad population on Hog Island (see comments under *Bufo woodhousii fowleri* account). This species has been reported from only one other barrier island outside the Virginia system (Gibbons and Coker, 1978).

Lampropeltis getula getula (Linnaeus)

The eastern kingsnake (see nomenclatural note in Frost and Collins, 1988) is known only from Smith Island (USNM); it is found on most of the barrier islands in North Carolina and South Carolina (Gibbons and Coker, 1978). This species was the second most abundant snake on Smith Island on 28 May 1986. All known specimens were found under boards in the grass habitat between the primary and secondary dunes. Kingsnakes are predators of rodents, other reptiles, and the eggs of some turtles (Knight and Loraine, 1986). We suspect its primary prey on the island are small rodents, *Coluber constrictor*, and possibly *Opheodrys aestivus*.

Nerodia sipedon sipedon (Linnaeus)

The northern water snake has been collected on Assateague (USNM), and Parramore (AMNH), and Smith (USNM) Islands. It has been observed on Chincoteague (W.A. Dunson, JCM, CAP), Wallops (Fowler, 1925) and Hog (Brady, 1925) Islands. Brady (1925) noted it was common around freshwater ponds and in salt marshes on Hog Island. Lee (1972) reported that it occurred in brackish and salt marshes but was uncommon on Assateague Island. Gibbons and Coker (1978) reported that this species or its southern ecological equivalent, *N. fasciata*, occurred on every barrier island studied.

Available specimens are phenotypically similar to mainland water snakes. The dorsal pattern consists of dorsal blotches that occur as bands on the anterior third of the body but break up and occur as alternating dorsal and lateral blotches on the posterior two-thirds. One specimen from Smith Island (USNM 22633, collected in 1894) lacks the alternating pattern; a strong crossbanded pattern is present. The only consistent difference from mainland Eastern Shore snakes is that there is more dark pigmentation on both the dorsum and venter. The posterior half of the venter of one specimen from Assateague Island (USNM 165917) is nearly black. Some insular populations of *Nerodia sipedon* have been found to consist of banded, patternless, and intermediate individuals (Camin and Ehrlich, 1958; Conant and Clay, 1963). A tidal marsh population in the Potomac River has been reported to be unbanded (Bulmer, 1985). Conant has found that dark pigmentation of the venter is of common occurrence among many populations from or near brackish habitats of coastal areas of both New Jersey and mainland Delmarva. Farther south, on the Outer Banks and along shores of the associated Sounds of North Carolina, melanism, both dorsally and ventrally, is commonplace (Conant and Lazell, 1973).

Little ecological information is available for barrier island water snakes. A note accompanying the 1899 Smith Island collection said the water snakes were "found in pools of brackish water preying on small fish". One (USNM 22633) also contained a *B. woodhousii fowleri* swallowed headfirst.

Opheodrys aestivus conanti Grobman

The barrier island green snake has been vouchered from eight of the Virginia barrier islands (Table 2, AMNH, CM, USNM, VCU) and observed on Wallops Island (Fowler, 1925); also Revel (Table 1). It probably occurs on all islands with grassland/shrub habitat. This species (*O. aestivus*) was reported from all of the Atlantic barrier islands studied by Gibbons and Coker (1978). Grobman (1984) examined specimens from the Virginia islands and available specimens from the Delmarva Peninsula, mostly Maryland, and concluded that the barrier island populations were sufficiently different from mainland populations to warrant subspecific recognition. This taxonomic distinction was based on the fewer number of ventral and subcaudal scales than in populations from the mainland. Our data confirm the difference; however, we recognize that specimens from mainland Eastern Shore of Virginia are needed before we can ascertain whether the differences are restricted to the islands or represent clinal variation along the peninsula.

Brady (1925) reported this snake to be common on Hog Island and neighboring islands where grassland communities existed. Lee (1972) reported only one green snake from Assateague Island. We found these snakes to be abundant under debris in the wrack zone (Cobb and Hog Islands) and in the pine-myrtle association on Parramore Island in 1947 and 1986. This species is sometimes found syntopic with *Storeria dekayi*. Mitchell and Pague are currently investigating other aspects of its ecology on Cobb Island.

Storeria dekayi dekayi (Holbrook)

Populations of northern brown snakes are known from Parramore (AMNH, CM, USNM), Hog (CM), and Cobb (USNMFS) Islands. Conant found this snake to be abundant on Parramore and Hog Islands in 1947. During 1948 he also encountered it on Parramore Island, but none was seen on Hog Island, which was visited two weeks after that island had been virtually completely covered by an exceptionally high tide, and salt water was standing almost everywhere. This species also occurs at Cape Hatteras, North Carolina (Gibbons and Coker, 1978). Island populations are phenotypically similar to populations on the Virginia mainland, in both pattern and scutellation (JCM and CAP, unpublished). We have found them under debris in the wrack zone and in a pine-cedar-myrtle association. Several specimens have what appeared to be earthworm remains in their stomachs. Other aspects of its ecology are being studied on Cobb Island.

Virginia valeriae valeriae Baird and Girard

Fowler (1925) reported the eastern earth snake from Hog Island, based on a specimen supposedly in the Academy of Natural Sciences of Philadelphia. The ANSP has no record of it, however (J.E. Cadle, pers. comm.). Dunn (1918) listed this species from Northampton County, apparently based on this specimen. Mitchell and Pague found none during a visit to Hog Island on 30 May 1986; neither did Conant during his visits to that island in 1947, 1948, and 1975. No localities are confirmed for the mainland Eastern Shore of Virginia (the three in Tobey, 1985 are erroneous), although they are recorded for the Eastern Shore of Maryland (Harris, 1975). This species should be listed as unverified from the Virginia barrier islands.

Table 3. Composition of the herpetofauna of the Eastern Shore and barrier islands of Virginia. The ninth island snake is the unverified *Virginia valeriae* from Hog Island.

| Group | Mainland | Islands | Percent |
|---------------------------------|----------|---------|---------|
| Frogs | 14 | 7 | 50.0 |
| Salamanders | 5 | 1 | 20.0 |
| All amphibians | 19 | 8 | 42.1 |
| Turtles | 12 | 11 | 91.7 |
| Turtles, minus sea turtles | 8 | 7 | 87.5 |
| Lizards | 3 | 2 | 66.7 |
| Snakes | 12 | 8 (9) | 66.7 |
| All reptiles | 27 | 21 | 77.8 |
| All reptiles, minus sea turtles | 23 | 17 | 73.9 |

DISCUSSION

The composition of the herpetofauna of the Virginia barrier islands heavily favors reptiles (Table 3). Of the amphibian fauna occurring on mainland Eastern Shore, only 42.1% is also found on the barrier islands, compared with 77.8% of the reptiles. The single species of salamander and all but one of the frogs are found only on the Assateague-Wallops cluster at the northern end of the island chain. Their absence on Smith Island is puzzling because that island encompasses most of the vegetative community types found on the northern cluster. The paucity of amphibians on the islands is undoubtedly related to the permeability of amphibian skin to water. Although numerous populations of amphibians, notably anurans, have been reported from brackish water habitats (Neill, 1958), survival in highly saline environments is low. Terrestrial island habitats are also xeric and few amphibians can tolerate such desiccating conditions. Most reptiles, on the other hand, are able to withstand short-term immersion in sea water because of the relative impermeability of the scale-covered epidermis (Lillywhite and Maderson, 1982). Their colonizing ability and persistence on barrier islands are reflected in the higher representation of the mainland Eastern Shore reptile fauna (73.9%, excluding sea turtles).

Several aspects of the herpetofauna on the Virginia barrier islands offer comparisons with the fauna on the coastal islands from North Carolina to Florida studied by Gibbons and Coker (1978). The frogs *Hyla cinerea* and *Rana utricularia*, both frequently found in brackish marshes in Virginia (JCM and CAP, pers. obs.), are found on most of the southeastern islands but are restricted to Assateague and Chincoteague Islands in Virginia. The mud turtle, *Kinosternon subrubrum*, occurs on nearly all of the Atlantic barrier islands, whereas the box turtle, *Terrapene carolina*, has been confirmed for only three Atlantic barrier islands (Gibbons and Harrison, 1981; Braswell, 1988; this study). The snapping turtle, *Chelydra serpentina*, absent from several of the apparently suitable southeastern islands, is found on all Virginia islands which have freshwater. The five-lined skink, *Eumeces fasciatus*, is absent from all of the Atlantic barrier islands despite its abundance on the mainland. The single species of small ground snake, *Storeria dekayi*, found on

several of the Virginia islands is known from only one other southeastern barrier island (Braswell, 1988). It is puzzling why the hognose snake, *Heterodon platirhinos*, has such a spotty occurrence on islands compared with its ubiquitous prey species, toads of the genus *Bufo*. Two snakes that are found on several of the southeastern islands (Gibbons and Coker, 1978; Gibbons and Harrison, 1981; Braswell, 1988) are notably absent from the Virginia islands, specifically *Thamnophis sauritus* and *Thamnophis sirtalis*. Speculations about the causes of such differences would be pointless without a full knowledge of the historical biogeography of all these island populations, man's influence, and the physiology and life history of each species. Such information should be obtained where possible.

Models of the formation of the Virginia barrier islands (Rice *et al.*, 1976 and references therein) offer insights into the origin of the herpetofauna on these islands. Three models have been used to describe island formation: (1) production of long shore sand bars away from the shore line, the deBeaumont-Johnson model; (2) successive elongation of a coastal sand spit, the Gilbert-Fisher model; and (3) the formation of coastal dune ridges that were subsequently isolated by rising sea level, the Hoyt-Godfrey model. Islands arising by the deBeaumont-Johnson model would have to be colonized completely by dispersal over salt water. Islands arising by processes described by the other two models have had mainland connections. The amphibian and reptile populations on these islands could originally have been parts of mainland populations that later became fragmented when the islands were separated by rising sea level. An example of the Gilbert-Fisher model is Currituck Spit, comprising Back Bay National Wildlife Refuge and False Cape State Park. This area harbors a large herpetofauna that is similar in many respects to the adjacent mainland fauna (Pague and Mitchell, 1982). Assateague Island may have been a spit connected to the mainland; its herpetofauna is the most diverse of any of the islands. An example of the Hoyt-Godfrey model is the Cape Henry area of Virginia Beach. This dune ridge system, now isolated from the mainland, contains a large herpetofaunal assemblage similar to the adjacent mainland (CAP and JCM, unpublished). The primary conclusion from these observations is that it may not be necessary to invoke dispersal over seawater to explain the origins of all the barrier island herpetofaunas.

If the herpetofaunas of the Virginia barrier islands were of mainland origin, then the probability is high that coastal processes and island dynamics have decreased the original number of species. The many changes on Hog Island are excellent examples of marine transgressions. The number of species remaining as a result of these processes may be a function of either distance from the mainland or island area, or both (MacArthur and Wilson, 1967). Our preliminary analysis indicates the linear relationship of species number (excluding sea turtles) to distance from the mainland for the Virginia barrier island group is negative and non-significant ($P = 0.572$). However, the linear relationship of species number to island area is positive and significant ($r^2 = 0.529$, $P = 0.017$). If we eliminate Assateague Island from the analysis because of the presence of man-made freshwater impoundments, the species-area correlation becomes non-significant ($P = 0.121$). Smith Island, despite its relatively small size, contains the second largest number of species in the Virginia barrier island group. This is probably because of the diversity of habitats on the island. Dueser and Brown (1980) found that rodent

diversity on the Virginia barrier islands was influenced most significantly by vegetation height and number of woody plant associations. Herpetofaunal species diversity may be explained by the number of habitat types on each island and the occurrence of freshwater. Gibbons and Coker (1978) found that the numbers of amphibians and reptiles (analyzed separately) for nine Atlantic coast barrier islands were significantly correlated with woodland area.

The impact of human habitation of the Virginia barrier islands on the amphibian and reptile fauna is undoubtedly significant but impossible to assess without information on historical occurrences. Nevertheless, it is probable that logging, livestock grazing, and farming (Graham, 1976) and controlled burning and creation of freshwater impoundments, as on Assateague Island (W.A. Dunson, pers. comm.), decreased the amount of forested land. These impacts increased types of habitat favorable to some species and decreased it for others. An increase in grassland and shrub habitats would be favorable to *Coluber constrictor*, *Opheodrys aestivus*, and *Storeria dekayi*. The increase in freshwater has undoubtedly favored an increase in anuran and turtle species diversity on Assateague Island. Forest-dwelling species, like *Elaphe obsoleta* and *Terrapene carolina*, would be negatively affected by loss of habitat. Humans certainly killed snakes on the islands just as they do virtually everywhere.

We concur with Gibbons and Harrison (1981) in that the most severe impact on terrestrial amphibians and reptiles stems from the removal of organic litter and ground cover in forests. These authors also point out the importance of shallow water sites to anuran breeding and larval development and that alteration of these sites for mosquito control would be detrimental. The loss of these features or any major vegetative community type would negatively affect herpetofaunal species diversity on the Virginia barrier islands.

Mitchell and Pague (in press) discuss the loss of habitat to agriculture and logging on mainland Eastern Shore, and some ways in which management efforts can conserve the herpetofauna. Loss of habitat will continue to have negative impacts on source populations from which the islands may be colonized. The predicted urban sprawl will certainly continue this process.

Our current knowledge of herpetofaunal species diversity on the Virginia barrier islands is limited to that obtained from numerous short-term visits to the islands. The potential increase in species numbers gleaned from the use of time-intensive methods (e.g., drift fences with pitfall traps), so well illustrated by Braswell (1988), justifies future field efforts.

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Longitudinal Surveys of the Beach Nesting and Colonial Waterbirds of the Virginia Barrier Islands

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ABSTRACT

Fourteen consecutive years of data (1975-1988) from beach nesting and colonial waterbird surveys on the Virginia barrier islands, Assawoman Island through Fisherman Island, revealed fluctuating numbers of adults of the 27 species surveyed. Consistency of personnel, survey techniques, and timing have been essential elements in the quality of this project. Factors effecting species counts such as nesting stage, habitat, numerical density and weather are discussed. Species which show trends of population increase are herring, laughing and great black-backed gulls, and great egret. Species which seem to be declining are cattle egret, little blue heron, tricolored heron and black-crowned and yellow-crowned night heron, glossy ibis, royal, common, Forster's, gull-billed, and least tern and black skimmer. Several species seem to show shifts in their breeding site selections. Cattle egrets seem to be moving away from barrier island sites to large colonies at Walker's Marsh at Chincoteague, Virginia. Herring and great black-backed gulls seem to be showing less use of marsh spoil islands (tumps) for nesting and more use of the barrier island dunes. Common and Forster's terns may also be nesting more away from the barrier islands.

INTRODUCTION

At the request of The Nature Conservancy a survey of the Virginia barrier islands, was conducted in 1975 to establish a data baseline for the number and distribution of beach nesting and colonial waterbirds (Williams, 1975). In this analysis 1975 data were compared to historical records. It was apparent that no consistent body of information for these birds existed for Virginia. With the support of the Virginia Coast Reserve of The Nature Conservancy and the Non-game Wildlife And Endangered Species Fund of the Virginia Department of Game and Inland Fisheries, the surveys have continued for 14 consecutive years, providing an extraordinary set of data for the Mid-Atlantic Coast.

Colonial and beach-nesting waterbirds serve as potential bioindicators. Their patterns of nesting distribution may reflect responses to naturally occurring phenomena such as barrier island growth, attrition, or relocation. These patterns may also signal unnatural disturbances from human intrusion during all or part of the nesting season. Changes in species numbers may be indicative of changes in environmental quality directly affecting reproductive success. Thus, a close, consistent, and systematic survey of these species over many years provides information

for management and possible intervention, such as the efforts initiated for piping (*Charadrius melodus*) and Wilson's plovers (*Charadrius wilsonia*) recovery.

Although several atlases for colonial waterbirds have been published since 1975 (Erwin, 1979; Erwin and Korschgen, 1979; Osborn and Custer, 1978) the data presented here provides the most comprehensive study for Virginia.

METHODS AND MATERIALS

The best survey technique depends on the nature and size of the colony and/or species involved. All of the islands were walked completely. These are: Asawoman, Metompkin, Cedar, Dawson Shoals, Parramore, Sandy, Chimney Pole Marsh, Hog, Rogue, Cobb, Little Cobb, Wreck, Ship Shoal, Godwin, Mink, Myrtle, Smith and Fisherman. For solitary nesters such as oystercatchers and piping and Wilson's plovers, birds were tallied as they were encountered. Careful effort was made to avoid count duplication in situations where several pairs may have been occupying adjacent nesting territories.

Colonial beach nesting species were counted from a distance with the aid of binoculars. An attempt was made to record the total number of adults for each species before the birds flushed. In most instances, counts were done by at least two individuals, numbers compared, and a final figure derived. For many beach colonies where incubation was occurring a total nest count was also made to substantiate the total adult count. At no time were colonies subjected to visitation that would have rendered eggs or young vulnerable to heat or predation from gulls. In large colonies, or where young have hatched, entry into the colony was avoided.

Dune nesting species (primarily herring, laughing and great black-backed gulls) were counted several times by more than one observer, combining both numbers of ground and flying individuals to determine the colony size. Large densely-packed gull colonies, such as the one found in the dune-swale of Wreck Island, involved meticulous counts of groups of individuals in the air, and extrapolating that to the area occupied by the birds overhead.

Large mixed species heron, egret, and ibis colonies, with vegetation four to five meters in height were entered by one or more people to flush the birds occupying the colony at the time. Counters were stationed on opposite sides of the colony and communicated via radio. Birds were counted as they flushed and/or flew over the colony. Subsequently, the counters compared numbers and derived a final figure for each species. Small mixed heronries where the vegetation was no more than two meters high were tallied from the periphery of the colony. The great egret colony on the western side of Fisherman Island, was censused using a total nest count.

The timing of the survey has consistently occurred during the downy-feathered young stage of nesting for the herons, egrets, and ibis. Thus, our numbers are influenced by the absence of adults out gathering food.

For each colony, the following data were recorded on standard forms: time of day, length of visit, habitat, nesting substrate, survey technique, total adult count and nesting stage for each species. Data forms were subsequently sent to the Colonial Bird Register at the Laboratory of Ornithology, Ithaca, New York.

Every effort has been made to establish uniformity in gathering data. The survey period has consistently occurred during the third to the fourth week in June.

Islands were censused by the same individuals each year, and census procedures were standardized within the group.

RESULTS

The information provided in Table 1 is a compilation of all of the data gathered over 14 years. The numbers represent total adult counts for the entire island chain for a given year survey. Table 2 provides information on the number of years each species has been recorded as nesting on each island. Wilson's and piping plover and oystercatcher data are not included in this table since accurate counts for these species were not taken during the first 3 years of the project. The survey techniques themselves have inherent sampling error and colony dynamics over the nesting season from mid-May into July are variable, often weather-dependent. We present these data as indicators of population trends with a consistent time frame from which further study can be designed.

DISCUSSION

Although most species appear to have stable though fluctuating breeding populations within the survey area, several species deserve special attention. Cattle egrets (*Bubulcus ibis*) have shown as much as a 94% decrease from a high of 540 in 1977 to a low of 35 in 1983. However, several thousands of these birds nest annually in a colony off the causeway near Chincoteague, VA and at Walker's Marsh both of which are outside the scope of our survey area. A similar pattern of decline (89%) for black-crowned night herons (*Nycticorax nycticorax*) from 1976-1988 may also be attributable to a geographic shift in the breeding population.

Green-backed herons (*Butorides striatus*) and yellow-crowned night herons (*Nycticorax violaceus*) are not as strictly colonial as other members of the family and are therefore more difficult to sample.

The white ibis (*Eudocimus albus*) was unknown as a breeding bird in Virginia until 1977 (Frohring and Beck, 1978). Since then it has been recorded in colonies in 8 of 12 surveys. The species has probably been present each year since 1977, and those years in which it was not recorded are a result of the survey technique.

Herring gull (*Larus argentatus*) and laughing gull (*Larus atricilla*) populations seem to be stable at present. Within the context of this study it appears that both groups have numerically increased. These species may have retreated from nesting on inland marsh spoil areas in tumps to the low dunes of barrier islands where substantial beach loss has occurred. The large laughing gull numbers actually represent only one colony as of 1988, where in previous years that colony was one of several found on three or four islands. On the other hand, the great black-backed gull (*Larus marinus*) has undergone a dramatic increase in its breeding population over the last 10 years. Not found as a breeding species when the study began, the 561 recorded in 1986 seems remarkable. Whether the gull species are having an impact on the breeding efforts of other species in Virginia, as has been so well established elsewhere (Drury 1965, 1973, 1974; Nisbet, 1978; Harris, 1965; Hatch, 1970; Burger and Lesser, 1978, 1979) is unknown.

The single most revealing evidence of change from this study is the 88% decline in the population of the gull-billed tern (*Sterna nilotica*) from 1975-1987. Although modest increases were noted in 1986 and 1988, the overall decline has

been dramatic. This decline is a possible indication of an environmental problem, especially in view of the insectivorous feeding habits of this species.

Common tern (*Sterna hirundo*) numbers experienced a 45-50% decline over the last four years and may reflect a shift in the breeding population to other locations in the state, especially the Hampton Roads Bridge Tunnel where 2,178 birds nested in 1988 (R.A. Beck, unpublished).

The least tern (*Sterna antillarum*) population has shown dramatic fluctuations over the study period and although the overall Virginia population may be stable, it appears the species may be declining on the barrier islands (Beck, 1990).

Our data for royal terns (*Sterna maxima*) are conservative when compared to the number of young banded by other researchers. Our visual counts at the densely packed colonies represent the presence of attending adults and are thus subject to the same type of error addressed in sampling mixed heronries. Although the royal tern breeding locations shift, the population appears to be relatively stable.

Likewise, the sandwich tern (*Sterna sandvicensis*) population seems stable, although dramatic fluctuations between 1981 and 1984 are curious. In most instances this species can be readily counted within the royal tern colonies where they prefer to nest. However, in situations where they are few in number in a densely packed, restless colony, finding the birds is almost impossible.

The Caspian tern (*Sterna caspia*) is at the limits of its breeding range in Virginia (Bent, 1921). Thus, the 2-8 nesting individuals encountered each year represent a marginal breeding effort.

Our census of Forster's terns (*Sterna forsteri*) is limited to their presence in habitats adjacent to the barrier island beaches. In Virginia this species prefers to nest on *Spartina* wrack which accumulates in marshes especially along small creeks. Though we actively seek out this species, it may be unrecorded for the survey because colonies could not be located within the survey area (i.e., 1975, 1978, 1986, 1986-1988). Our data may indicate a severe decline for this species. In fact, the data may be a reflection of shifts in the location of the breeding effort that is dependent on the tidal accumulation of nesting substrate. In 1986, 29 colonies were found on the seaside of the Eastern Shore totalling 1,830 individuals. All of these colonies were on marsh or spoil, and none were on barrier islands (M. Byrd, unpublished).

Although modest fluctuations in the numbers of black skimmers (*Rhynchops niger*) are apparent, it appears that this species may be declining on the Virginia barrier islands. Given that over 1,000 skimmers nested between Wallops and Assateague Islands (K. Terwilliger, pers. comm.) in 1988 and that several hundred bred in Hampton Roads in 1988 (R. A. Beck, unpublished), the apparent decline may simply be a redistribution.

Gochfeld (1978) and Erwin (1979) pointed out a strong nesting association between nesting black skimmers and common terns. The decline in the skimmer population on the barrier islands may be directly related to the decline of the common tern previously mentioned.

A special effort to count oystercatchers (*Haematopus palliatus*) was not actually started until 1979. Numbers prior to that were either inconsistently gathered or not gathered at all. Since 1979 it seems apparent that the species is maintaining a stable population on the barrier islands.

TABLE 1. Total number of adults observed per year for 27 species of colonial and beach-nesting avian species on the Virginia barrier islands.

| SPECIES | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | Mean | CV |
|---------------------|------|------|-------|------|-------|------|-------|-------|------|-------|-------|-------|-------|-------|-------|-----|
| Green-backed Heron | 34 | 32 | 24 | 4 | 13 | 43 | 80 | 44 | 75 | 60 | 21 | 12 | 48 | 7 | 36 | 66 |
| Little Blue | 148 | 296 | 276 | 173 | 57 | 110 | 206 | 326 | 100 | 115 | 213 | 150 | 75 | 111 | 168 | 48 |
| Cattle Egret | 482 | 476 | 540 | 93 | 278 | 278 | 306 | 89 | 35 | 87 | 242 | 142 | 134 | 123 | 236 | 68 |
| Great Egret | 252 | 364 | 330 | 99 | 291 | 255 | 406 | 551 | 606 | 659 | 373 | 411 | 329 | 423 | 382 | 37 |
| Snowy Egret | 1192 | 2330 | 1196 | 245 | 364 | 332 | 772 | 776 | 376 | 731 | 655 | 611 | 728 | 313 | 759 | 69 |
| Tri-Colored Heron | 860 | 1364 | 956 | 293 | 497 | 382 | 700 | 1004 | 275 | 415 | 389 | 436 | 664 | 254 | 606 | 53 |
| Blk.-Crm. N. Heron | 1138 | 2780 | 2317 | 765 | 1143 | 836 | 840 | 1456 | 639 | 973 | 1082 | 850 | 540 | 314 | 1120 | 58 |
| Yel.-Crm. Heron | 46 | 108 | 78 | 68 | 105 | 74 | 113 | 75 | 119 | 93 | 60 | 63 | 39 | 24 | 76 | 37 |
| Glossy Ibis | 772 | 2534 | 628 | 320 | 481 | 389 | 705 | 964 | 578 | 637 | 742 | 556 | 463 | 304 | 720 | 74 |
| White Ibis | - | - | 4 | 0 | 6 | 0 | 2 | 2 | 2 | 0 | 2 | 2 | 0 | 4 | 2 | 91 |
| Brown Pelican | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 345 | 92 | 312 | 289 |
| Herring Gull | 1320 | 3932 | 2950 | 936 | 1429 | 2785 | 2312 | 3772 | 3489 | 1985 | 2403 | 8306 | 3662 | 3959 | 3089 | 56 |
| Laughing Gull | 3730 | 9810 | 10920 | 9151 | 17027 | 4920 | 13608 | 18188 | 9466 | 16383 | 19624 | 22286 | 18440 | 29680 | 14517 | 47 |
| Gr. Blk.-Back. Gull | 0 | 6 | 0 | 6 | 13 | 24 | 56 | 74 | 128 | 109 | 186 | 561 | 386 | 280 | 131 | 125 |
| Gull-billed Tern | 2228 | 2000 | 1092 | 955 | 737 | 959 | 1122 | 970 | 712 | 578 | 270 | 475 | 26 | 498 | 919 | 61 |
| Common Tern | 5218 | 6710 | 8496 | 3605 | 3347 | 5003 | 5260 | 3001 | 5219 | 5135 | 1843 | 2220 | 2240 | 2885 | 4299 | 43 |
| Least Tern | 766 | 886 | 1013 | 429 | 407 | 795 | 1869 | 550 | 1381 | 1217 | 717 | 1413 | 884 | 731 | 933 | 43 |
| Royal Tern | 4800 | 1330 | 9360 | 5962 | 3866 | 7326 | 5738 | 5200 | 8500 | 5772 | 7166 | 5910 | 6886 | 3656 | 5819 | 34 |
| Sandwich Tern | 18 | 28 | 30 | 80 | 2 | 34 | 34 | 4 | 140 | 24 | 18 | 80 | 20 | 24 | 38 | 94 |
| Caspian Tern | 2 | 2 | 2 | 2 | 2 | 4 | 2 | 6 | 4 | 6 | 2 | 8 | 8 | 8 | 4 | 59 |
| Black Skimmer | 7520 | 8811 | 10708 | 4824 | 5577 | 6970 | 9598 | 6303 | 5809 | 5233 | 3406 | 3780 | 3491 | 4448 | 6177 | 36 |
| Forster's Tern | 0 | 436 | 294 | 6 | 139 | 96 | 234 | 166 | 292 | 484 | 59 | 0 | 0 | 0 | 158 | 102 |
| Oyster Catcher | 528 | - | - | 81 | 1239 | 746 | 1151 | 1184 | 1223 | 1274 | 1079 | 1054 | 923 | 1004 | 957 | 35 |
| Piping Plover | 78 | - | - | 42 | 121 | 68 | 88 | 129 | 125 | 101 | 95 | 95 | 114 | 119 | 98 | 25 |
| Wilson's Plover | 58 | - | - | 21 | 51 | 20 | 41 | 61 | 52 | 46 | 18 | 63 | 64 | 43 | 45 | 36 |
| Nighthawk | - | - | - | - | - | 15 | 5 | 5 | 2 | 2 | 3 | 2 | 1 | 4 | 4 | 92 |
| Horned Lark | - | - | - | - | - | - | -9 | 25 | 10 | 8 | 5 | 1 | 1 | 7 | 8 | 86 |

TABLE 2. Number of years of nesting occurrence for each island 1975-1988. (Assawoman - AS; Metompkin - ME; Cedar - CE; Dawson Shoal - D; Paramore - PA; Sandy - SA; Chimney Pole - CP; Hog - HO; Rogue - RO; Cobb - CO; Wreck - WR; Ship Shoal - SS; Godwin - GO; Mink - MI; Myrtle - MY; Smith - SM; Fisherman - FI)

| | AS | ME | CE | DS | PA | SA | CP | HO | RO | CO | LC | WR | SS | GO | MI | MY | SM | FI |
|----------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| G-B Heron | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 14 | 6 | 0 | 0 | 0 | 4 |
| Little Blue | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 3 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 14 |
| Cattle Egret | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 14 | 0 | 1 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 14 |
| Great Egret | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 14 | 2 | 7 | 0 | 14 | 1 | 0 | 0 | 0 | 0 | 14 |
| Snowy Egret | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 14 | 2 | 7 | 0 | 14 | 2 | 0 | 0 | 0 | 0 | 14 |
| Tri-C. Heron | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 14 | 2 | 7 | 0 | 14 | 2 | 0 | 0 | 0 | 0 | 14 |
| Blk-CN Heron | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 14 | 1 | 7 | 0 | 14 | 2 | 0 | 0 | 0 | 0 | 14 |
| Yel-CN Heron | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 1 | 6 | 0 | 13 | 0 | 0 | 0 | 0 | 2 | 14 |
| Glossy Ibis | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 14 | 2 | 7 | 0 | 14 | 0 | 0 | 0 | 0 | 0 | 14 |
| White Ibis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 6 |
| Brn. Pelican | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Herring Gull | 0 | 14 | 0 | 0 | 1 | 4 | 13 | 4 | 0 | 12 | 0 | 13 | 3 | 0 | 0 | 0 | 2 | 14 |
| Laugh. Gull | 0 | 13 | 0 | 0 | 0 | 2 | 4 | 1 | 0 | 3 | 0 | 14 | 0 | 1 | 1 | 0 | 1 | 8 |
| Gr. BlkB. Gull | 0 | 8 | 0 | 0 | 0 | 1 | 11 | 0 | 0 | 7 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 11 |
| Gull-B Tern | 2 | 14 | 8 | 6 | 4 | 1 | 3 | 14 | 0 | 12 | 7 | 7 | 14 | 0 | 0 | 11 | 13 | 2 |
| Common Tern | 1 | 14 | 10 | 12 | 5 | 3 | 7 | 14 | 0 | 14 | 9 | 11 | 14 | 0 | 0 | 12 | 13 | 10 |
| Least Tern | 4 | 14 | 14 | 0 | 3 | 2 | 0 | 14 | 0 | 13 | 3 | 4 | 14 | 0 | 0 | 10 | 13 | 3 |
| Royal Tern | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 12 |
| Sand. Tern | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 3 | 0 | 0 | 0 | 1 | 8 |
| Caspian Tern | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 8 | 0 | 0 | 0 | 2 | 2 |
| Blk. Skimmer | 0 | 14 | 6 | 14 | 3 | 3 | 5 | 14 | 0 | 12 | 8 | 9 | 14 | 0 | 0 | 11 | 13 | 6 |
| Forst. Tern | 0 | 10 | 0 | 0 | 0 | 5 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 2 |

The piping plover (*Charadrius melodus*) has been the subject of much study (Williams *et. al.*, 1988; Patterson *et al.*, 1988), and appears to be rather stable as a breeding bird in Virginia. The Wilson's plover (*Charadrius wilsonia*), on the other hand, seems to show trends of stability and decline, a phenomenon that deserves further study. It should be noted that data for these two species were not gathered in 1976 or 1977.

SUMMARY AND CONCLUSIONS

Fourteen consecutive years of data from ground surveys of the beach nesting and colonial birds of the Virginia barrier islands reveal fluctuations in all populations. Sampling problems due to the nesting stage of some species and the nesting locations of others may contribute to the variation in the data. Further analysis on an island by island basis may provide insight into the population dynamics of these breeding birds.

The survey documents apparent increases in the three gull species and apparent declines in gull-billed, common and least terns, and black skimmers. Reasons behind these changes need to be elucidated for management purposes. There are indications that declines in common and least terns, cattle egrets, black-crowned night herons and black skimmers may represent shifts in the breeding locations of these species away from the Virginia barrier islands.

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Status of the Peregrine Falcon (*Falco peregrinus*) on the Virginia Barrier Islands

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ABSTRACT

Reintroduction of peregrine falcons (*Falco peregrinus*) to the barrier islands and adjacent areas through the technique of hacking began in 1978. Since 1978, 110 falcons have been released at coastal sites with a successful fledging and dispersal rate of 83%. Population models are presented to predict the growth of this founding population of peregrines. Because of subsequent variation in one major parameter used in the model, number of released birds, the model only suggests a range of population size. The present number of known adult pairs of peregrines is ten, near the minimum level predicted in 1983 for 1988. Success of these breeding pairs appears adequate to sustain the population. Evaluation of the viability of this population can only be made in the future.

Key words: Endangered species, *Falco peregrinus*, peregrine falcon, reintroduction, Virginia barrier islands

INTRODUCTION

The peregrine falcon (*Falco peregrinus*) is essentially cosmopolitan in its distribution (Brown and Amadon, 1968). Three races have been described in North America (White, 1968a, 1968b): *F. p. pealei*, *F. p. tundrius* and *F. p. anatum*. *Falco p. pealei* is a large, dark, sedentary form inhabiting the island chains of the Pacific Northwest. *Falco p. tundrius* is a paler-colored, smaller, highly migratory form with a breeding distribution limited to the Nearctic tundra region. *Falco p. anatum* is a large, forest-inhabiting race that is variable in its migration behavior. Its range spans the continent, intergrading with *tundrius* to the north and limited to north-central Mexico in the south. Peregrines which habitually nested in Virginia were an *anatum* subpopulation referred to as the Appalachian peregrine, and the population was comprised of individuals larger and darker than the other subpopulations of the race (White, 1968b).

The existence of 24 historical peregrine eyries of this population in the Virginia Appalachians was listed by Hickey, (1942) and Alva Nye (pers. comm.). Nesting was documented at two additional sites on the coast (Jones, 1946). The Virginia population was thought to winter on the coast, including the barrier islands. In addition, the coast and barrier islands are on the primary migration route of the highly migratory tundra race (Brown and Amadon, 1968). The barrier islands, thus, historically, provided habitat for two different populations of peregrine falcons.

The population of peregrine falcons in the United States east of the Mississippi River was estimated to reach peak numbers of 350 breeding pairs (Hickey, 1942). The decline and eventual extirpation of the eastern peregrine was attributed to the

biological concentration of organochlorine pesticide residues such as DDT and related compounds (Peakall, 1976). The last nesting peregrine in Virginia was gone by the mid-1960's (Hickey, 1969).

In 1975, the U.S. Fish and Wildlife Service appointed an Eastern Peregrine Falcon Recovery Team to develop a Recovery Plan (Bollengier *et al.*, 1979) which detailed the actions necessary to restore the peregrine in the east and to protect historical sites. The Plan depends on establishing a new population of peregrines by introducing captive-produced falcons into the wild (Barclay and Cade, 1983). In 1970, the Division of Biological Sciences and the Laboratory of Ornithology at Cornell University established a captive breeding program to develop techniques for eventually providing a source of falcons for reintroduction into the vacant eastern breeding range (Cade, 1974). The first young peregrines were produced in 1973 and since 1976 more than 50 young have been raised each year (Cade and Fyfe, 1978). Captive propagation was successful enough by 1975 to begin reintroductions in that year (Cade, 1980). Breeding birds came from several races and geographic areas (Barclay and Cade, 1983). This paper deals with this effort to reintroduce falcons to Virginia as a breeding population rather than with either fall migrants or the small wintering population on the islands.

METHODS

Field Methods - The Cornell facility effort has been the source of all birds introduced to the barrier islands. Peregrines were released into the wild using a technique known as "hacking", a process modified from traditional falconry practice as described by Mitchell (1900, referenced in Barclay and Cade, 1983). Nine hack towers were constructed, of which eight remain: six are located on the barrier islands, one located on an island in southern Chesapeake Bay and one located at Back Bay National Wildlife Refuge (Figure 1). This technique consisted of placing broods of three to six young falcons approximately 28-30 days old in a protective hack box at the release site. Falcons were fed daily on either coturnix quail or chickens and released at approximately 40-45 days of age when they were capable of flight. Food was supplied at the hack box until the young falcons became independent and dispersed from the site. Further details on this technique may be found in (Cade and Temple, 1977) and Sherrod and Cade (1983).

Peregrines were first hacked in 1975 (Barclay and Cade, 1983). The hacking technique was designed for use at or near historic eyries with the expectation that when birds reached breeding age, they would return to nest (Bollengier *et al.*, 1979). Predation at historical cliff sites in New Hampshire and New York by great horned owls (*Bubo virginianus*) suggested that the number of peregrines dispersing normally would increase if releases occurred in habitats not usually frequented by that species. In Virginia, therefore, hack sites were established on coastal islands, Chesapeake Bay marsh islands, Back Bay National Wildlife Refuge, and one urban setting (a nine story rooftop in Norfolk, Va.) (Fig. 1). These locations provide open terrain for hunting, a suitable prey base, minimal human disturbance, and safety from predators (Barclay, 1980). These sites are relatively permanent and can be used as nest sites by returning birds.

All released peregrines were individually marked with numbered aluminum U.S. Fish and Wildlife Service bands. Auxiliary plastic bands with alpha-numeric

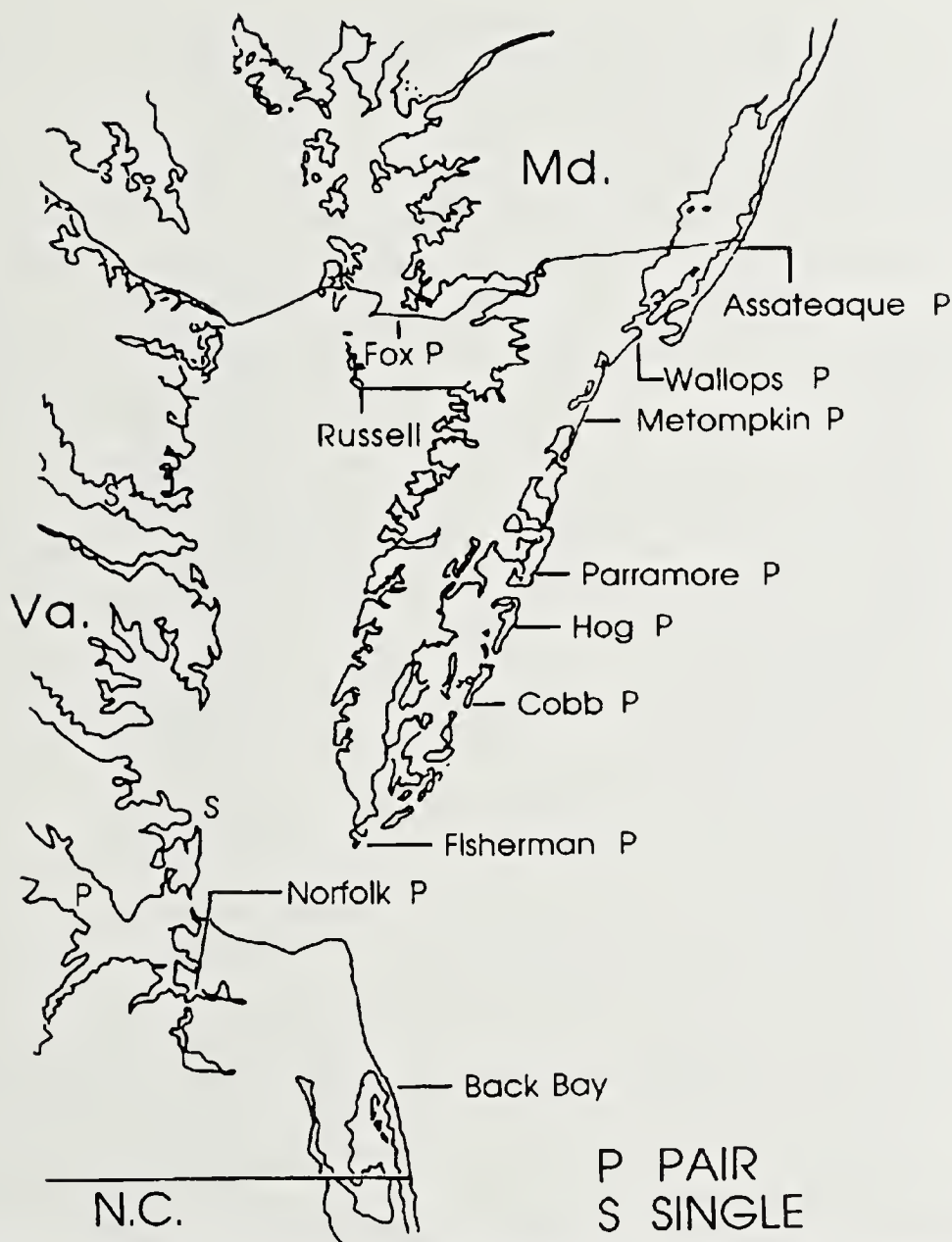


FIGURE 1. Named hach sites indicating pairs of peregrines at these and other sites, 1988. Established pairs of falcons (P) occurred on 10 sites and established solitary adults (S) on 3 sites in 1988.

codes were also used, except in 1980 releases. Two birds released in 1979 carried tail mounted radio transmitters. As many banded, breeding adults as possible were trapped by use of harnessed pigeons in 1987 to determine age and origin of these birds.

Model - A stochastic model for population growth developed by Grier (1979) was used to assist in population estimates and to project results of the reintroduction program. The model simulates the growth of an existing or reintroduced population using known or assumed parameters. The incorporation of random chance within given probabilities for reproduction, sex of individuals, and mortality realistically approximates the unpredictability of small founding populations. The model parameters include:

- 1) monogamous or polygamous breeding pattern,
- 2) age that breeding begins,

- 3) maximum number of young per female,
- 4) mean number of young per annual breeding attempt,
- 5) mean number of young per successful breeding,
- 6) first year mortality rate,
- 7) mortality rate of third year and older animals,
- 8) limit (if any) on number of breeding pairs per year,
- 9) number (if any) and sex of first-year animals released per year, and,
- 10) number (if any) and sex of older animals released per year.

Simulation results include number of animals of given age classes present at the beginning and end of any year. The stochastic nature of the program produces variable results due to random chance. For this reason, five simulations are run for every year and the mean and range of possible outcomes are presented. The model does not, however, account for emigration and immigration of peregrines.

Other parameters included 60% first-year mortality and 20% subsequent annual mortality. These mortality rates are conservative estimates which include pre-dispersal losses and are based on band recovery data from wild populations (Enderson, 1969) and returns of released peregrines (Barclay, 1980). Means of 1.5 young per nesting attempt and 2.5 young per successful nesting attempt were used in the model. Several studies (Mebs, 1960 referenced in Barclay, 1980; Herren, 1969) indicate that this productivity is conservatively realistic. Forty percent of nesting attempts produce no young which is largely a reflection of the low reproductive success of second year birds which are included as breeders in this model. Beebe (1960) found approximately 60 percent breeding success of all recorded attempts in the *F. p. pealei* population of Queen Charlotte Islands. The number of breeding pairs in coastal Virginia will probably be limited by the number of towers or other suitable nesting substrata which are present in a given year. The number of pairs which can attempt breeding is limited to 14 for this series of simulations. That is the maximum number of hack/breeding towers that could be erected in the immediate future. It does not take into account other possible nesting substrata such as bridges or buildings. The number of pairs present in any simulation is defined by the number of the sex which is limiting in any given year.

RESULTS

Hacking Results - Sixteen releases of captive produced peregrines were made at six island sites (Table 1) from 1978-1985. Two additional releases were made in Norfolk in 1981 and 1982 and one release at Back Bay in 1982 (Table 2). A total of 110 birds was released at these 9 sites between 1978 and 1985.

Hacking success is measured by the percentage of released peregrines that become independent with respect to food and normally disperse from the hack site. For consistency, birds not seen after four weeks post-release are assumed independent unless individual evaluation or other evidence suggests otherwise. The success rate of peregrine releases from 1978-1985 in Virginia was 84 percent. The success and mortality by site and year appear in Tables 1 and 2.

Mortality and other losses incurred during hacking at 9 sites ranged from 0% to 71%. The greatest single loss of five young at Russell Island in 1985 was due to predation by a great horned owl. The losses of 3 young at Assateague Island in

TABLE 1. Fledging success of peregrine falcons released on the barrier and Chesapeake Bay islands, 1978-1985.

| Year | Island Location | Number Released | Number Fledged | % of Young Fledged |
|------|-----------------|-----------------|----------------|--------------------|
| 1978 | Cobb | 5 | 3 | 60 |
| 1979 | Cobb | 5 | 5 | 100 |
| 1980 | Cobb | 5 | 5 | 100 |
| | Fisherman | 5 | 3 | 60 |
| 1981 | Assateague | 6 | 3 | 50 |
| | Great Fox | 6 | 6 | 100 |
| | Cobb | 6 | 6 | 100 |
| 1982 | Russell | 6 | 6 | 100 |
| | Great Fox | 6 | 6 | 100 |
| 1983 | Cobb | 7 | 7 | 100 |
| | Russell | 7 | 7 | 100 |
| | Great Fox | 4 | 1 | 25 |
| 1984 | Russell | 6 | 6 | 100 |
| | Cobb | 5 | 5 | 100 |
| | Parramore | 7 | 7 | 100 |
| 1985 | Russell | 7 | 2 | 29 |
| | TOTALS | 93 | 78 | 84 |

1981 and three young at Great Fox Island in 1983 were due to harassment and killing by previously-hacked adult falcons.

The moderate pre-dispersal mortality of all Virginia releases ((17%) is probably due to several factors, namely, the choice of predator-free hack sites and the dedication of hack attendants. In several cases, young peregrines were rescued from predicaments that would have proven fatal if not for human intervention.

Only one peregrine shooting is known to have occurred in eastern Virginia since 1978. An unbanded individual (implying a wild peregrine) was found shot near Norfolk, Virginia. The possibility exists that more peregrines are being shot and not reported since it is an unlawful activity.

Population Estimation and Projection - Determining total population numbers of peregrines resident on the barrier islands or in Virginia, generally, is difficult due to the high mobility of the young birds and our inability to follow widely dispersed individuals throughout the year. Estimating the number of breeding-age adults is easier due to the tendency for these birds to remain territorial at suitable breeding sites, ie., hack towers and bridges. In 1988, 10 established adult pairs and three adult unpaired birds (2 males and one female) were known to exist in Virginia. The locations of adult pairs and singles are shown in Figure 1. Although two of the single birds comprised a hypothetical eleventh pair, the individuals occupied separate territories approximately 40 km apart. Both birds remained sedentary

TABLE 2. Fledging success of all eastern Virginia peregrine falcon releases.

| Years | Location | Number Released | Number Fledged | % of Young Fledged |
|-----------|------------------|-----------------|----------------|--------------------|
| 1978-1985 | Barrier Islands | 93 | 78 | 84 |
| 1980 | Downtown Norfolk | 6 | 5 | 83 |
| 1981 | Downtown Norfolk | 4 | 4 | 100 |
| 1982 | Back Bay N.W.R. | 7 | 7 | 100 |
| TOTALS | | 110 | 91 | 83 |

throughout the year making it improbable that they paired with each other. Each bird currently represents a potential pair at its respective site.

The stochastic model was used to project estimates of population size and to evaluate results of the reintroduction program (Fig. 2).

This model was based on the number of peregrines released through 1982 and assumed that nine first year male and nine first year female peregrines would be released per year to 1990. With a limitation on the number of breeding pairs in coastal Virginia (14), the model indicates a current population in Virginia of 33-48 peregrines (mean = 41.8) including 12-17 pairs (mean = 14.0). Yearly projected population numbers from 1978 to 1990 are presented in Table 3.

An identical model was run without limiting the number of breeding pairs to determine maximum population numbers. The mean number of breeding pairs present in 1990 under those circumstances was 18. This indicates that 18 nest sites would be needed by 1990 to allow the mean number of potential pairs to attempt breeding.

Figure 3 shows the simulated growth of a Virginia peregrine population which is subject to 50% hatch first-year mortality and 15% subsequent year mortality. Other parameters in this model are identical to the growth simulation displayed in Figure 2. The reduction of hatch year mortality by 17 percent and post-hatch year mortality by 25% in the growth simulations (Figs. 2 and 3) produces a significantly higher number of pairs and total birds present in the year 1990. The projected 1990 population estimate in the simulation is also significantly affected (Table 4). As noted earlier, studies of mortality by band recovery methods indicate that some peregrine populations may experience mortality rates as low as 55 percent (Shor, 1970) for first-year birds.

Peregrine Movements - Information was compiled from band recoveries on movements of 12 Virginia released peregrines and four peregrines released out of state and recovered in Virginia through 1982 (Table 5). Most of these records are due to trapping efforts of raptor banders. The movement of Virginia-released

TABLE 3. Population growth simulation A data. Sixty percent hatch-year and twenty percent after-hatch-year mortality was assumed. Pairs are defined by number of limiting sex.

| Year | Birds released | <u>Total birds present</u> Simulations: | | | | | | | <u>Pairs present</u> Simulations: | | | | | | |
|------|----------------|--|----|----|----|----|------|-------|--------------------------------------|----|----|----|----|------|-------|
| | | 1 | 2 | 3 | 4 | 5 | Mean | Range | 1 | 2 | 3 | 4 | 5 | Mean | Range |
| 1978 | 3 | 1 | 1 | 3 | 1 | 2 | 1.6 | 1-3 | 0 | 0 | 0 | 0 | 0 | 0.0 | 0-0 |
| 1979 | 5 | 2 | 5 | 5 | 1 | 4 | 3.4 | 1-5 | 0 | 0 | 1 | 0 | 1 | 0.8 | 0-1 |
| 1980 | 18 | 6 | 12 | 14 | 9 | 8 | 9.8 | 6-14 | 0 | 2 | 2 | 0 | 2 | 1.2 | 0-2 |
| 1981 | 19 | 15 | 17 | 16 | 11 | 14 | 14.6 | 11-17 | 0 | 4 | 4 | 2 | 3 | 2.6 | 0-4 |
| 1982 | 19 | 17 | 15 | 20 | 16 | 23 | 18.2 | 15-23 | 3 | 5 | 7 | 4 | 5 | 4.8 | 3-7 |
| 1983 | 18 | 29 | 21 | 22 | 18 | 29 | 23.8 | 18-29 | 5 | 5 | 8 | 7 | 10 | 7.0 | 5-10 |
| 1984 | 18 | 32 | 23 | 27 | 18 | 26 | 25.2 | 18-32 | 9 | 8 | 8 | 8 | 10 | 8.6 | 8-10 |
| 1985 | 18 | 38 | 27 | 31 | 22 | 36 | 30.8 | 22-38 | 13 | 6 | 11 | 7 | 10 | 9.4 | 6-13 |
| 1986 | 18 | 43 | 26 | 32 | 30 | 32 | 32.6 | 26-43 | 15 | 8 | 9 | 10 | 11 | 10.6 | 8-15 |
| 1987 | 18 | 40 | 30 | 43 | 38 | 35 | 37.2 | 30-43 | 13 | 10 | 11 | 12 | 12 | 11.6 | 10-13 |
| 1988 | 18 | 42 | 33 | 48 | 43 | 43 | 41.8 | 33-48 | 14 | 12 | 17 | 12 | 15 | 14.0 | 12-17 |
| 1989 | 18 | 36 | 36 | 55 | 45 | 52 | 44.8 | 36-55 | 14 | 7 | 21 | 15 | 17 | 14.8 | 7-21 |
| 1990 | 18 | 39 | 28 | 62 | 52 | 55 | 47.2 | 28-62 | 14 | 10 | 21 | 16 | 20 | 16.2 | 10-21 |

peregrines appears to be consistent with the wandering typical of juvenile birds. The longest movement to New York entailed 520 km over 11 months, in contrast to several birds that were captured a few months after release in the vicinity of their hack tower. Of the nine recoveries of Virginia peregrines, five were southerly, two were northerly, and two easterly. Any inland movements remain undetected with the possible exception of unidentified males on a building in Richmond from 1983-1986 and on a bridge on the Rappahannock River from 1986-1988.

During the breeding season of 1987, in collaboration with the Peregrine Fund, breeding adults were trapped at sites in Maryland, Virginia, and New Jersey to determine their origins. Twelve adults were captured which were breeding in Virginia or were of Virginia origin (Table 6). Five birds nesting in Virginia were of Virginia origin and three had immigrated from either Maryland or New Jersey. Four birds nesting in New Jersey had originated in Virginia. These limited data indicate a wide movement of birds, suggesting that the reestablished peregrine

TABLE 4. Comparison of simulated populations in 1982 and 1990 with 60/20 (Sim A) and 50/15 (Sim B) mortality rates.

| | Simulation A (n = 5) | Simulation B (n = 5) | t(8) | P |
|---------------------|----------------------------|----------------------------|------|-------|
| 1982 | | | | |
| Pairs present | 4.8 ± 1.44 | 7.6 ± 4.30 | 2.95 | 0.05 |
| Total birds present | 18.2 ± 3.27 | 31.0 ± 5.15 | 4.69 | 0.01 |
| 1990 | | | | |
| Pairs present | 16.2 ± 4.49 | 40 ± 4.30 | 8.56 | 0.001 |
| Total birds present | 47.2 ± 13.59 | 108 ± 5.12 | 9.46 | 0.001 |

population should be considered as a mid-Atlantic, and not as a Virginia, population.

Breeding Success and Population Viability - The first successful breeding attempt of peregrine falcons in Virginia for more than 20 years occurred at the Assateague Island hack tower in 1982. Both of these birds were banded and were considered to be hacked birds, although they were not trapped for identification. The number of known adult pairs each year since 1982 has grown with a total of 10 pairs in 1988 (Table 7).

DISCUSSION

Mortality - As observed in most avian groups, mortality of first-year peregrines is the highest of any age class. Estimates of first-year mortality rate of wild peregrines vary from 55% (Shor, 1970) to 80% (Mebs, 1960 referenced in Barclay, 1980). Barclay (1980) determined a 72 percent success rate of releases in the eastern U.S. from 1975 to 1979. First-year mortality of 70% is accepted for North American peregrine populations (Enderson, 1969). First-year mortality can be divided into pre- and post-dispersal periods. The post-dispersal period is commonly thought to be a more difficult time as it requires the young birds to hunt successfully. Post-dispersal young are also prone to encounter more hazards due to their increased range. Pre-dispersal birds, however, are subject to many dangers. The fledging, or first flight, is an important phase in avian development and tends to be hazardous. Injuries that occur due to lack of judgment or skill may doom a young peregrine. Data are lacking on the pre-dispersal mortality for wild peregrines, but estimates do exist for a congener with similar population dynamics. Prairie falcons (*Falco mexicanus*) in Idaho experience pre-dispersal mortality rates varying from 12-26% (Kochert, 1976; Peterson, 1976 referenced in Barclay, 1980). These figures are minimal estimates as every individual was not accounted for due to the lack of radio telemetry.

Biologists have much less control over post-dispersal mortality of released peregrines. Hunting is a behavior which can only be perfected through experience.

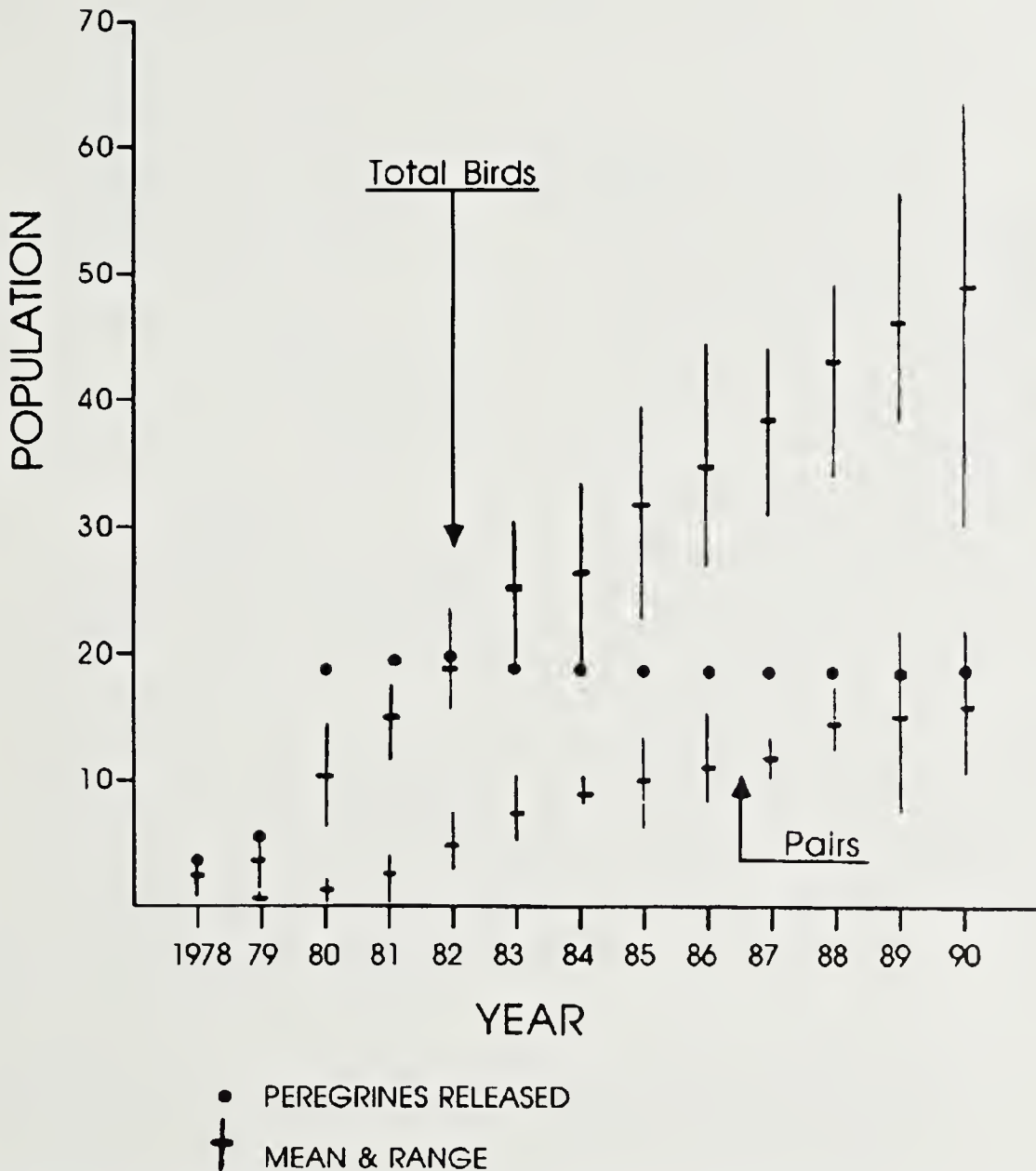


FIGURE 2. Projected growth of Virginia peregrine population assuming 60% hatch-year and 20% after-hatch-year mortality.

For this reason, food is made available to the released peregrines at the sites for up to six weeks post-release. Food reduction is also employed to further stimulate hunting without risking starvation. Hunting proficiency of hacked birds is possibly enhanced by the amount of practice each bird experiences. The high density of potential prey, especially migrating shorebirds, on the barrier islands of Virginia increases prey encounters.

Human persecution continues to be an important cause of post-dispersal mortality. Half of the band recoveries in earlier studies by (Enderson, 1969; Shor, 1970) were attributed to shooting. Peregrines released by hacking are unavoidably subject to human contact although techniques are used to minimize the chances of developing human-food relationships. Nevertheless, hacked peregrines sometimes seem less wary of humans than their wild counterparts. Coupled with the large amount of gunning which occurs in the Chesapeake Bay area, losses of peregrines to unscrupulous hunters is a distinct possibility.

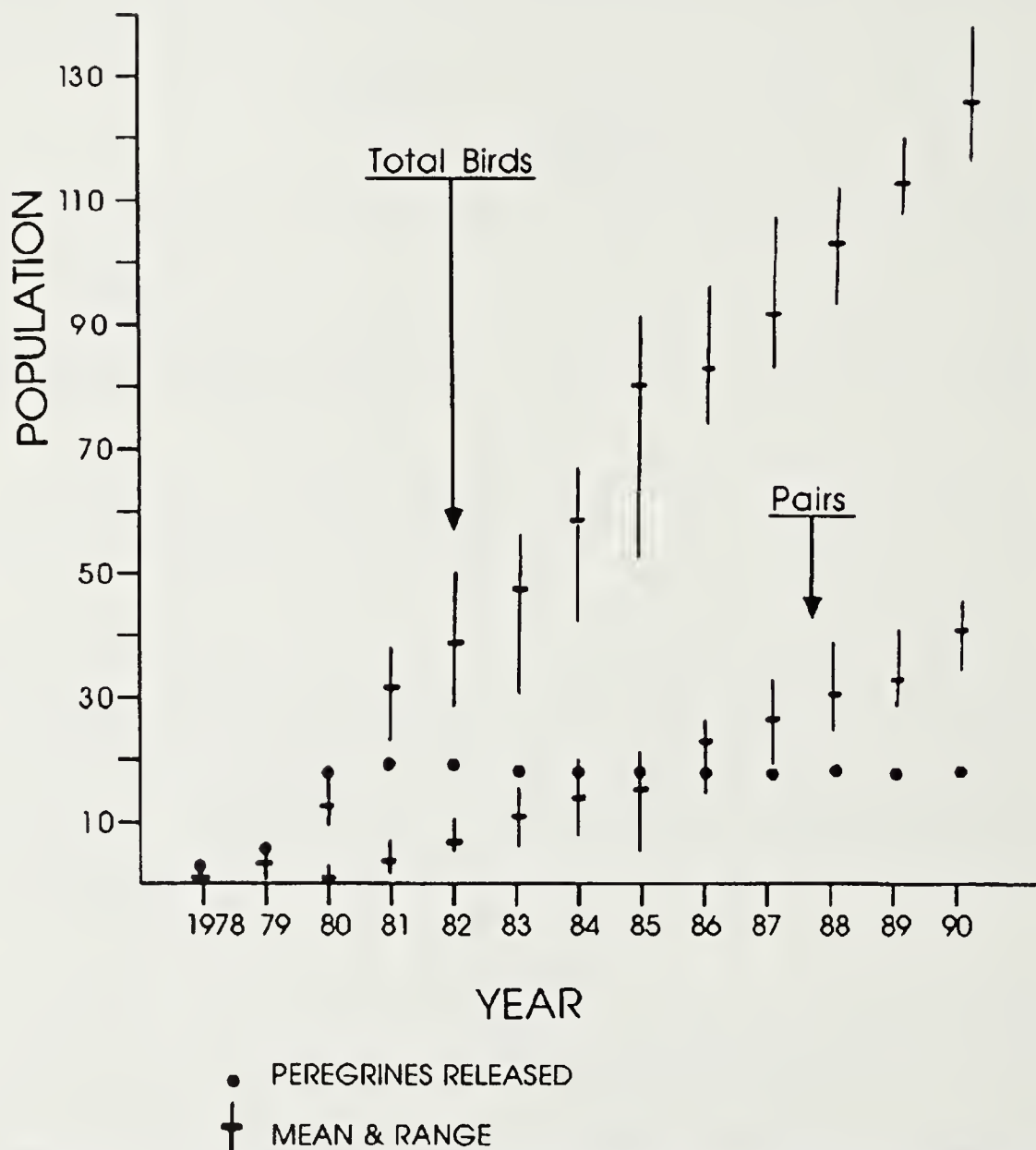


FIGURE 3. Projected growth of Virginia peregrine population assuming 50% hatch year and 15% after-hatch-year mortality.

After reviewing band recovery data, Barclay (1980) concluded that peregrines hacked in the eastern U.S. are not subject to heavier shooting pressure than wild peregrines. Evidence does exist that the amount of raptor shooting in Europe has decreased since 1949 (Newton, 1979) possibly due to a more conservation minded public and protective legislation.

Population Status - Analysis of survivorship tables shows that mortality rate affect population growth to varying degrees, partly dependent upon the age at maturity of the species. Populations of animals such as the bald eagle (*Haliaeetus leucocephalus*) which do not breed until their fourth year are extremely affected by slight changes in mortality rates. Peregrines generally do not breed successfully until their third year. The breeding attempts of subadult birds are usually included in reproductive figures. The relatively high frequency of unsuccessful breeding attempts reported (40%) is probably reflective of a high percentage of attempts by

TABLE 5. Recovery of individual peregrine falcons hacked in Virginia.

| Band number | Sex | Hack site/year | Recovery |
|--------------|-----|--------------------|--|
| 576-89280 | M | Cobb/78 | Trapped Fisherman 9/78 |
| 576-89270 | M | Cobb/78 | Returned Cobb (seen) 5/79-7/79 |
| 987-01322 | F | Cobb/79 | Trapped Sandy Hook, NJ 4/15/80 Found dead Quogue, NY 4/24/80 |
| 816-40327 | M | Cobb/80 | Returned Cobb (seen) 5/81-6/81 Trapped Fisherman 10/5/81 |
| 816-40322 | M | Assateague/80 | Trapped Assateague 9/24/80 |
| 987-01343 | F | Assateague/80 | Trapped Assateague 9/24/80 Trapped False Cape 10/1/80 Trapped Assateague 10/8&10/13/80 |
| 987-49509F | F | Great Fox/81 | Trapped Assateague 9/18/81 |
| 987-49507 | F | Great Fox/81 | Trapped Corolla, NC 9/30&1/19/81 |
| 987-49533 | F | Great Fox/82 | Seen at Horntown, VA 7/18/82 |
| * 987-01361 | F | South Marsh, MD/80 | Resident on Assateague 5/81-10/81 Trapped Assateague 10/81 |
| * 987-49559 | F | South Marsh, MD/82 | Trapped Wise Point, VA 9/25/82 |
| ** 987-49598 | F | Assateague/82 | Trapped Back Bay, VA 9/16/82 |
| 987-49551 | F | Great Fox/82 | Trapped Cape May, NJ 9/18/82 |
| * 987-49564 | F | South Marsh, MD/82 | Trapped Assateague 10/3/82 |
| * 987-49577 | F | Silver Lake, NY/82 | Trapped Assateague 10/11/82 |

* Hacked outside Virginia; recovered in Virginia.

** Young of "natural" nesting in Virginia.

subadults. Survivorship tables do indicate that relatively small changes in mortality rates have profound effects on peregrine population growth (Young, 1969).

The above model allows one to determine whether populations, defined by certain parameters can be self-supportive. When no artificial release of animals occurs, natural reproduction must be sufficient to compensate for mortality or the population declines. Repeated simulations indicate that a peregrine population experiencing 60% hatch-year and 20% subsequent year mortality rates cannot be self-supportive at documented reproductive rates. This implies that stable wild populations which display these reproductive rates probably are subject to lower mortality rates than those calculated by band recovery studies. More study is needed accurately to determine breeding parameters of re-established peregrine falcon populations.

One of the parameters utilized in these models, the release of 18 peregrines per year until 1990, has not been realized. All releases on the barrier islands were terminated after 1985. Despite this, the currently known number of 10 adult pairs appears close to the lower limit of adult pairs as projected by the simulation A of the model (Table 3).

Movements - Virginia is within the wintering range of a migrant population of peregrines. Peregrines sighted from September through June, therefore, are pos-

TABLE 6. Location of breeding peregrine falcons in Virginia, or of Virginia origin, 1987.

| Breeding Location | Sex | Hack site/year | Naturally hatched/year |
|----------------------------|-----|----------------------|------------------------|
| Great Fox Island, VA | F | Cobb/81 | |
| Cobb Island, VA | F | Cobb/83 | |
| Parramore Island, VA | M | | Chincoteague N.W.R./83 |
| Metomkin Island, VA | F | Smith Island. Md./84 | |
| Chincoteague, N. W. R., VA | M | Cobb/78 | |
| Chincoteague, N. W. R., VA | F | | Sea Isle, N.J./83 |
| Hog Island, Va. | M | Parramore/84 | |
| Fisherman Island, VA | M | Smith Island, Md./84 | |
| Sedge Island, NJ | F | Russell/83 | |
| Manahawkin, NJ | F | Parramore/84 | |
| Brigantine, N. W. R., NJ | F | | Chincoteague N,W.R./82 |
| Tuckahoe, NJ | F | Russell/84 | |

sibly birds that are migrating or wintering and not released birds. Since the commencement of Virginia peregrine hacking in 1978, summer sightings have dramatically increased, attesting to the efficiency of hacking. Only banded peregrines can be identified as individuals and then only under excellent viewing conditions or when trapped. For this reason, most sightings are of unidentified peregrines. Peregrines seen between June 1 and August 15 or exhibiting breeding behavior may be safely assumed to be released birds or their progeny. Due to the Virginia recovery of several birds released in other states, resident birds in Virginia cannot be assumed to be Virginia releases. For population considerations, emigration and immigration were assumed to be equal.

Although young peregrines wander widely, the ultimate test of hacking success is the return to and establishment of, successfully breeding adults at the site of origin or at suitable sites in other areas.

Population Viability - The production of young by nesting peregrines in Virginia is consistent with or higher than the parameters utilized in the population model and higher than the eastern population in general (Gilroy, 1987). The model is a useful predictor of population growth. The known number of adult pairs appears to be near that predicted by the model, although there likely are unknown pairs which would increase the total.

Since releases are no longer planned for the coast, a fundamental question exists as to the viability of this population. At three barrier island sites in Virginia, there has been clear evidence of mate loss followed by rapid replacement of that individual. This also has occurred at other sites in the east (Marty Gilroy, pers. comm.), suggesting that there are surplus individuals available to enter the breeding population. In Virginia, reproduction appears adequate to provide replacements but as seen in Table 6, there is considerable movement involved.

TABLE 7. Breeding success of peregrine falcons in Virginia % Pairs

| Year | Known Pairs | Pairs Attempting Nesting | Pairs Successful % Attempting Nesting | Which Attempted Nesting | Successful Which Att. Nesting | Young Produced | Young Fledged Per Nesting Attempt | Young Fledged Per Successful Nesting Attempt |
|--------|-------------|--------------------------|---------------------------------------|-------------------------|-------------------------------|---------------------|-----------------------------------|--|
| 1982 | 1 | 1 | 100 | 1 | 100 | 4.0 | 4.00 | 4.00 |
| 1983 | 2 | 1 | 50 | 1 | 50 | 4.0 | 4.00 | 4.00 |
| 1984 | 4 | 2 | 50 | 2 | 100 | 4.0 | 2.00 | 2.00 |
| 1985 | 7 | 2 | 29 | 2 | 100 | 7.0 | 3.50 | 3.50 |
| 1986 | 7 | 4 | 57 | 3 | 75 | 7.0 | 1.75 | 2.33 |
| 1987 | 9 | 5 | 56 | 4 | 80 | 14.0 ⁽¹⁾ | 2.80 | 3.50 |
| 1988 | 10 | 5 | 50 | 4 | 80 | 16.0 ⁽²⁾ | 2.40 | 3.00 |
| TOTALS | 40 | 50 | 50 | 17 | 85 | 54 | 2.70 | 3.17 |

(1) Two young in captivity but included in calculations
(2) Four young died of disease, not included in calculations

An adequate evaluation of this population probably can be made only after several years in which no further artificial introduction of young has been made in the Mid-Atlantic region.

Management Considerations - It is essential that disturbance during the breeding season be minimized. Since most of the breeding pairs are located on the barrier islands, the future of those islands is critical. There are increasing pressures for human use of the islands. The extent to which this can be controlled is important to the continued success of peregrines in that habitat.

The most important limiting factor for breeding adults would appear to be adequate nesting sites. The original hack towers continue to be the most important sites on the coast. It is essential that they be repaired and well maintained in the future. New sites on unusual structures such as buildings and bridges must be identified and adequate management, such as nest box installation, implemented.

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Status and Distribution of the Least Tern in Virginia - 1975 to 1988

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ABSTRACT

Small, scattered breeding colonies of the least tern (*Sterna antillarum*) are found on over-wash areas on the beaches of the barrier islands of the Eastern Shore of Virginia. Two large colonies occur in the Tidewater region of Virginia on the western shore of the Chesapeake Bay at Grand View Beach in Hampton and Craney Island in Portsmouth. Data from 14 consecutive breeding seasons indicate changes in the geographic locations and fluctuations in population sizes of the least tern in Virginia. These data show a fluctuating population on the barrier islands with an overall decreasing trend. The colonies at Grand View Beach and Craney Island are increasing in number and currently represent more than half of the total Virginia population. Mammalian, avian, and human disturbances have influenced least tern production and in some cases prevented successful nesting. Least tern populations have responded positively to protection of nesting habitat. Several management techniques have been successfully implemented to attract terns to specific areas at the Craney Island site.

INTRODUCTION

The least tern (*Sterna antillarum*) breeds in scattered colonies along the Atlantic coast of the United States from Maine to Florida, along the Gulf coast to southern Texas (Erwin, 1979), and the Pacific coast from California to southern Mexico (Dement'ev & Gladohov, 1969). In the interior of the United States the least tern is found along the Mississippi drainage where it nests on sandbars and islands of the larger rivers (Hardy, 1957). In Virginia, the least tern breeds on the barrier islands on the seaward margin of the Delmarva Peninsula and on certain beaches located along the west side of the lower Chesapeake Bay.

Bailey (1913) and Murray (1952) recorded the least tern as a breeding species in Virginia. During the last quarter of the nineteenth century, however, least terns along the East coast were virtually exterminated as a result of the decorative use of tern feathers and skins in the women's millinery trade. Plume hunters invaded terneries and slaughtered adult terns by the thousands. The skins were shipped to New York City where they sold for ten cents each (Saunders, 1969). Bent (1921) reported as many as 100,000 terns killed each year along the Atlantic coast during peak harvesting years. In one 3-day period, 2,800 least terns were killed on Cobb

Island, Virginia, with 1,400 taken in a single day. By the turn of the century the least tern population had declined precipitously. Bailey (1913) reported that the Virginia population had been reduced to only a few scattered breeding pairs by the early 1900's.

Legislation was passed in 1918 to protect migratory birds [Federal Migratory Bird Treaty Act]. With protected status least tern populations began to recover. By the 1920's and 1930's much of the east coast had been recolonized. Pearson *et al.* (1942) estimated that the North Carolina population was approximately 25,000 in June 1939. Nisbet (1973) estimated the Massachusetts population reached 1,500 during a peak period between 1945 and 1954. There are no known reports on the least tern population in Virginia during this recovery period.

Colonies of least terns continued to increase throughout the east coast until the 1950's. Between 1950 and 1970, however, decreasing numbers of least terns were again noted (Downing, 1973). In Massachusetts (Nisbet, 1973) and along the South Carolina and Georgia coasts (Tomkins, 1959), all populations were reported to be declining.

Within the Chesapeake Bay and major river systems of eastern Virginia, few least tern colonies were reported from the 1950's to the 1970's, and these were scattered throughout the region (Scott, 1956). In Virginia, estimates of the total least tern population in the 1970's were approximately 1,500 birds per year (Downing, 1973; Akers, 1975; Erwin *et al.*, 1979).

Typical least tern nesting habitat has been described as a broad, flat, open beach area with little or no vegetation (Marples and Marples, 1934). The substrate may be sand, broken shells, or shingle (a combination of crushed shell and pebble) (Bent, 1921; Mosley, 1976). The colony site is usually situated close to water where high winds from spring storms combined with high tides often destroy entire colonies by washing out the nests (Witherby *et al.*, 1941).

The objectives of the study were to determine the status of the least tern in Virginia, to detect changes in population numbers, and determine if population shifts have occurred.

STUDY AREAS

The three primary locations of least tern colonies in Virginia are the barrier islands on the Eastern Shore; Grand View Beach, Hampton; and Craney Island, Portsmouth. From north to south, the islands censused were: Assawoman, Metompkin, Cedar, Dawson Shoal, Parramore, Sandy, Chimney Pole Marsh, Hog, Rogue, Cobb, Little Cobb, Wreck, Ship Shoal, Godwin, Mink, Myrtle, Smith and Fisherman. These 18 barrier islands are under varying degrees of protection and preservation by the Virginia Coast Reserve of The Nature Conservancy, Chincoteague National Wildlife Refuge of the U.S. Fish and Wildlife Service, Assateague Island National Seashore of the National Park Service, the Virginia Department of Game and Inland Fisheries, and private ownership.

Located on the western shore of the Chesapeake Bay, the Grand View Beach site (N 37° 06.3', W 76° 17.2'), under the management of the Department of Hampton Parks, differs from the Eastern Shore habitat in that it is to some extent protected from direct ocean waves and is infrequently washed over by spring storms and high tides.

Craney Island (N 36° 55', E 76° 22') is a man-made, dredge-spoil disposal site operated by the Norfolk District of the U. S. Army Corps of Engineers since the 1950's and is an atypical tern site for Virginia. This site covers about 41 square kilometers and extends 6.5 kilometers into Hampton Roads from the original shoreline. Colonies are located on relatively high areas where the substrate tends to be drier than the surrounding flats. These sites are not affected by tidal action, but nests are at a greater risk of flooding by heavy rain because of the high silt content of the substrate.

Small groups of least terns arrive on the coast of Virginia in late April and early May over a period of seven to ten days. The colonies have synchronous reproduction where young hatch by the second week in June if weather conditions are favorable.

METHODS

Barrier Islands - Each year from 1975 to 1988, the Virginia barrier islands have been censused in conjunction with the annual colonial nesting bird survey for the Colonial Bird Register (Williams, 1975). The barrier islands data were collected by the authors, working as a team, during this 14-year period. Based on experience and observations prior to 1975, the third and fourth weeks of June were selected as the most likely time to find eggs, young, and renesting attempts. All barrier island surveys were conducted within this time period.

In each survey, team members walked the entire beach area (mean high water to primary dunes including wash-over areas) of all 18 islands looking for nests and birds. Three to four days were required to cover the approximately 84 kilometers of shoreline from Fisherman Island to Assawoman Island. The location of each tern colony site was marked on U.S. Geological Survey topographical charts (7.5 minute series).

The specific phase of the breeding cycle was identified and recorded for each colony. For colonies of fewer than 100 nests, an attempt was made to count each nest. After the nest count, the observer(s) walked through the colony to flush and count the number of adult birds. With larger colonies, multiple observers recorded their individual estimates of nests and the number of adults before and after the birds were flushed. The individual estimates of adult birds and nests were compared and reconciled in the field.

The duration of colony disturbance was kept to a minimum. The observer(s) moved steadily through a colony without lengthy pauses to permit the birds first disturbed to return to their nests and thereby minimize stress on the eggs and young.

Grand View Beach and Craney Island - Grand View Beach and Craney Island were studied in detail by one of the authors (Akers). Field work began in 1973 with weekly or daily observations of these colonies from April 15 to July 30 (Akers, 1975). Since 1975, the same intensive observation schedule has been maintained by the same observers.

Adults were counted weekly until the peak of hatching. Typically, this procedure provided five independent counts of adults per breeding season. Multiple nest counts were also conducted until hatching began. With the onset of hatching, young were counted during each weekly survey. Fledged young were also recorded.

Since 1977, a total of 1,971 young have been banded at Grand View Beach. Because of the potential danger of driving young into nearby ditches and ravines, fewer than 50 young were banded over the course of this study at Craney Island.

In 1985 the United States Army Corps of Engineers, the Department of Biology at the College of William and Mary, and Virginia Department of Game and Inland Fisheries cooperated to establish potential tern nesting sites. During each winter, the superintendent of the Craney Island Project for the Corps of Engineers identified anticipated low use areas not required for dredging operations in the coming spring and early summer. The superintendent and one of the authors (Beck) conducted on site inspections to assess each area for its potential as a least tern breeding colony site. The most promising areas were designated on the Craney Island Site Plan. The Corps then improved the selected sites as necessary by elevating them for better drainage. The areas were then covered with sand and white shell fragments to attract the terns. The Corps then limited vehicular traffic around the boundaries of these areas. This cooperative effort is expected to continue.

From 1985 to 1988, the Craney Island colony has consisted of three to five separate groups. Beginning in 1986, 50 wooden least tern decoys were constructed and displayed in each of three potential nesting sites. The purpose of this experiment was to attract adult least terns to specific locations. From 1986 through 1988, the terns used two of the three sites. All tern colonies were identified and posted. To prevent disturbance by vehicular traffic the Corps constructed circumferential trenches and blocked roads passing through terneries when necessary.

RESULTS

The location of least tern colonies censused in the 14 years of this study, status of the sites (active/inactive), and number of active sites each year are given in Fig. 1. The presence of territorial adults and nests with eggs or young determined an active site. The total number of adults at the three primary locations plus Chincoteague National Wildlife Refuge each year are given in Table 1. Data from Chincoteague National Wildlife Refuge (Ailes, 1985) are also included in Fig. 1. Census data from 1978 to 1988 at that site have been used with our data to obtain a more complete understanding of least tern population trends and movement on the Eastern Shore of Virginia.

Cedar, Hog, Metompkin, and Ship Shoal Islands had breeding colonies in all 14 years, and colonies were on Cobb and Smith Islands in all but one year.

The barrier islands and Chincoteague population data exhibit extreme variability in numbers from year to year (Fig. 2). Abundance increased dramatically in 1981 followed by an overall decreasing trend through 1988. Data for the Grand View Beach colony also exhibited large changes in numbers from year to year and a sharp rise in population after 1980 (Fig. 3). The overall trend was toward increasing numbers. The Craney Island colony exhibited a doubling in numbers in 1981 after recolonization of this site in 1980 (Fig. 4). From 1981 to 1985, there was a gradual increase each season followed by a drop in 1986. Significant increases occurred in 1987 and 1988.

In Fig. 5, all data sets have been combined to show the total least tern population in Virginia from 1975 to 1988. There is clearly a significant change in the population

| NAME OF GEOGRAPHIC LOCATIONS | SURVEY YEAR | | | | | | | | | | | | | |
|------------------------------------|-------------|----|----|----|----|----|----|----|----|----|----|----|----|----|
| | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 |
| VIRGINIA BARRIER ISLANDS | | | | | | | | | | | | | | |
| ♦ ASSAWOMAN | - | - | ■ | - | - | - | - | - | - | - | - | ■ | ■ | ■ |
| ♦ CEDAR | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| ♦ CHIMNEY POLE MARSH | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| ♦ COBB | ■ | ■ | ■ | ■ | - | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| ♦ DAWSON SHOAL | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| ♦ FISHERMAN | - | - | - | - | ■ | ■ | ■ | - | - | - | - | - | - | - |
| ♦ GODWIN | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| ♦ HOG | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| ♦ LITTLE COBB | | ■ | | ■ | ■ | | | | | | | | | |
| ♦ METOMPKIN | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| ♦ MINK | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| ♦ MYRTLE | ■ | ■ | ■ | - | - | ■ | ■ | | ■ | ■ | ■ | ■ | ■ | ■ |
| ♦ PARRAMORE | ■ | ■ | ■ | - | - | - | - | - | - | - | - | - | - | - |
| ♦ ROGUE | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| ♦ SANDY | - | - | - | - | - | - | - | ■ | - | - | - | - | - | - |
| ♦ SHIP SHOAL | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| ♦ SMITH | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | - | ■ | ■ |
| ♦ WRECK | - | - | - | ■ | ■ | - | - | - | - | - | ■ | - | - | ■ |
| CRANEY ISLAND | ■ | ■ | ■ | - | - | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| GRAND VIEW ISLAND | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| CHINCOTEAGUE NWR | - | - | - | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| NUMBER OF ACTIVE LOCATIONS | 10 | 11 | 11 | 10 | 10 | 11 | 11 | 10 | 10 | 10 | 11 | 10 | 11 | 11 |

FIGURE 1. Locations of active least tern colonies surveyed from 1975 to 1988. (Data from the Chincoteague National Wildlife Refuge/Assateague Island provided by I. Ailes, unpublished report).

occurring with the 1981 breeding season. A straight line, least squares fit to these data from 1975 to 1980 has a slight negative slope indicating an annual decrease of about 18 birds (Slope = -18.46, $R^2 = 0.04$). After the large population jump in 1981, a straight line, least squares fit to the 1981-1988 data, indicates an annual decrease of 88 birds (Slope = -88.24, $R^2 = 0.32$).

A similar fit to the combined least tern population west of the Chesapeake Bay indicates an annual decrease of about 12 birds during the 1975-1980 period (Slope = -12.57, $R^2 = 0.08$). However, in the period from 1981 to 1988, there is an annual increase of approximately 61 terns (Slope = 61.76, $R^2 = 0.65$).

The ratio of the number of least terns on the west side of the Chesapeake Bay to the total population in Virginia shows an apparent shift in the population from the barrier islands to the west during the latter half of this study (Fig. 6). From 1981 to 1988, the growth of the population west of the Bay increased approximately 4% each year (Slope = 0.04, $R^2 = 0.80$). In addition, more than half of the least tern population of Virginia was located west of the Bay in 1985, 1987, and 1988.

Of the 1,971 least tern young banded at Grand View Beach and Crane Island, only ten have been recaptured since 1977.

TABLE 1. Adult population sizes of least terns in Virginia, 1975-1988.

| Year | Virginia Barrier Islands | Chincoteague National Wildlife Refuge | Grand View Beach, Hampton | Craney Island, Portsmouth | Virginia Total |
|------|--------------------------------|--|---------------------------------|---------------------------------|-------------------|
| 1975 | 766 | | 350 | 150 | 1266 |
| 1976 | 886 | | 160 | 160 | 1206 |
| 1977 | 1013 | | 160 | 120 | 1293 |
| 1978 | 429 | 20 | 400 | 0 | 849 |
| 1979 | 407 | 350 | 300 | 0 | 1057 |
| 1980 | 795 | 120 | 300 | 100 | 1315 |
| 1981 | 1869 | 200 | 600 | 200 | 2869 |
| 1982 | 550 | 854 | 600 | 200 | 2204 |
| 1983 | 1381 | 392 | 900 | 220 | 2893 |
| 1984 | 1217 | 210 | 600 | 222 | 2249 |
| 1985 | 717 | 104 | 800 | 250 | 1871 |
| 1986 | 1413 | 43 | 950 | 200 | 2597 |
| 1987 | 884 | 22 | 970 | 300 | 2176 |
| 1988 | 731 | 120 | 650 | 510 | 2011 |

DISCUSSION

The estimation of large flocks of birds on the wing, under varying light and weather conditions, is a skill developed slowly over time and with much practice. Precise counting of flocks of greater than 100 birds is usually not possible and the variation between the estimates of multiple observers increases with the size of the flock. Each of the authors have a minimum of 20 years' experience in both land and aerial surveys of terrestrial and pelagic avian species. The individual experience and the experience of working as a team over many years tends to minimize observer error.

Typically, we are able to obtain counts which deviate by no more than approximately 5% for flocks in flight of 100 to perhaps 300 birds under good conditions. At higher numbers the estimates may differ by 10%. Even under good observing conditions, discrepancies can arise between the estimates of multiple observers. The procedure used consistently by the authors has been to average the estimates from two observers; drop the high or low estimate of three observers and average the two remaining; and drop both the high and low estimate when there are four observers and average the two remaining numbers.

Estimation of the number of nests within a least tern colony is also a skill refined over time. In Virginia, the size of least tern colonies are generally less than 100 nests. Experience has shown that our individual estimates are consistent to within approximately 5%.

Although many obvious adverse factors on the population can be delineated, there exists a spectrum of others that may or may not play a role in the large

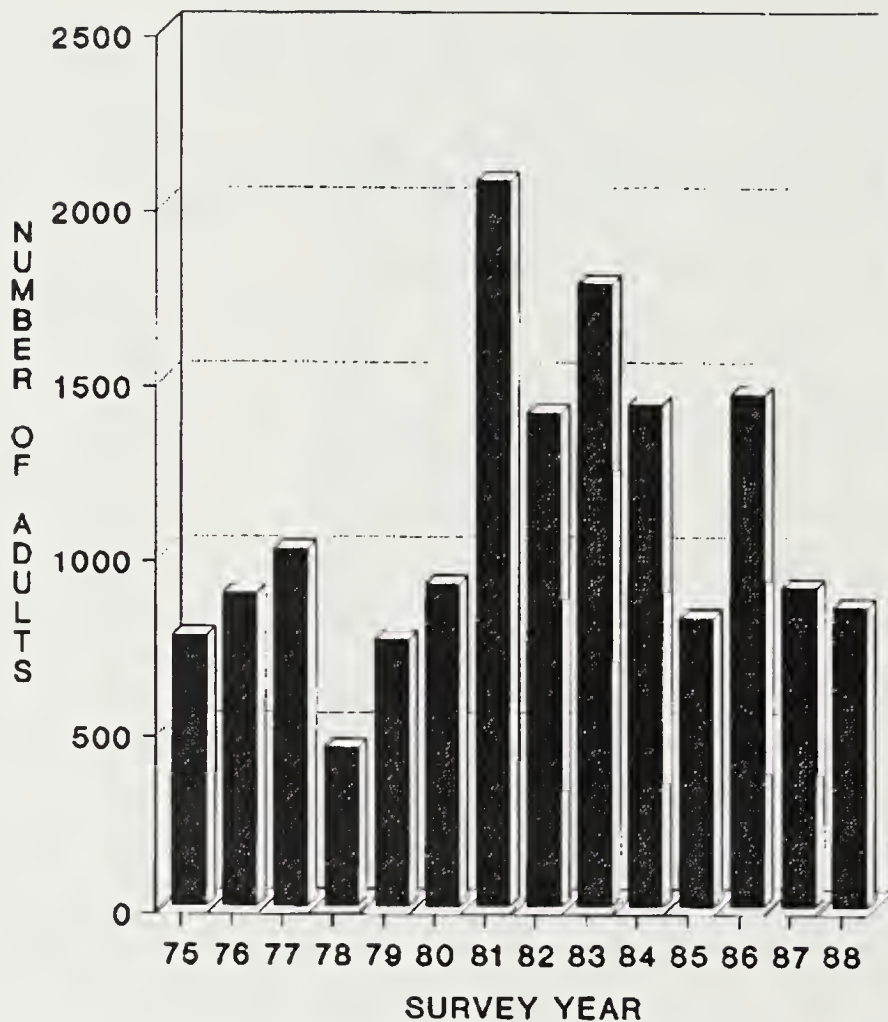


FIGURE 2. Combined number of adult least terns observed in yearly surveys on the barrier islands and the Chincoteague National Wildlife Refuge from 1975 to 1988. (Data from the Chincoteague National Wildlife Refuge covers the years from 1978 to 1988).

variations observed in the duration of this study. In the following discussion, those factors adversely affecting the colonies observed during our surveys will be addressed in an attempt to understand the population variability in Virginia.

Barrier Islands - Least tern colonies located on the Virginia barrier islands are subjected to a wide range of adverse conditions, both natural and man-related, that can destroy large numbers of young and eggs, and force relocations of colonies from year to year. Under favorable climatic conditions, however, dramatic increases in the population can occur in a single breeding season (see Fig. 2).

Weather plays a paramount role in nesting success or failure. The habitat preference of the least tern exposes nesting sites to the full impact of high winds, driving rains, and high seas. Flooding is the single greatest threat with its potential to obliterate entire colonies in a few hours. Although least terns will re-nest two or three times in a single season, repeated wash-outs have occurred at critical intervals with devastating effect on the colonies. In the 1978 and 1979 breeding seasons, large storms lasting several days repeatedly pounded the barrier islands, wreaking havoc on the colonies through wash-over and cold rain. The adverse effects of these storms are clearly reflected in sharp population declines in these two consecutive years for the lowest numbers observed in this study (Fig. 2). As an indication of the severity of these storms in 1978-79, Little Cobb Island was obliterated and remained

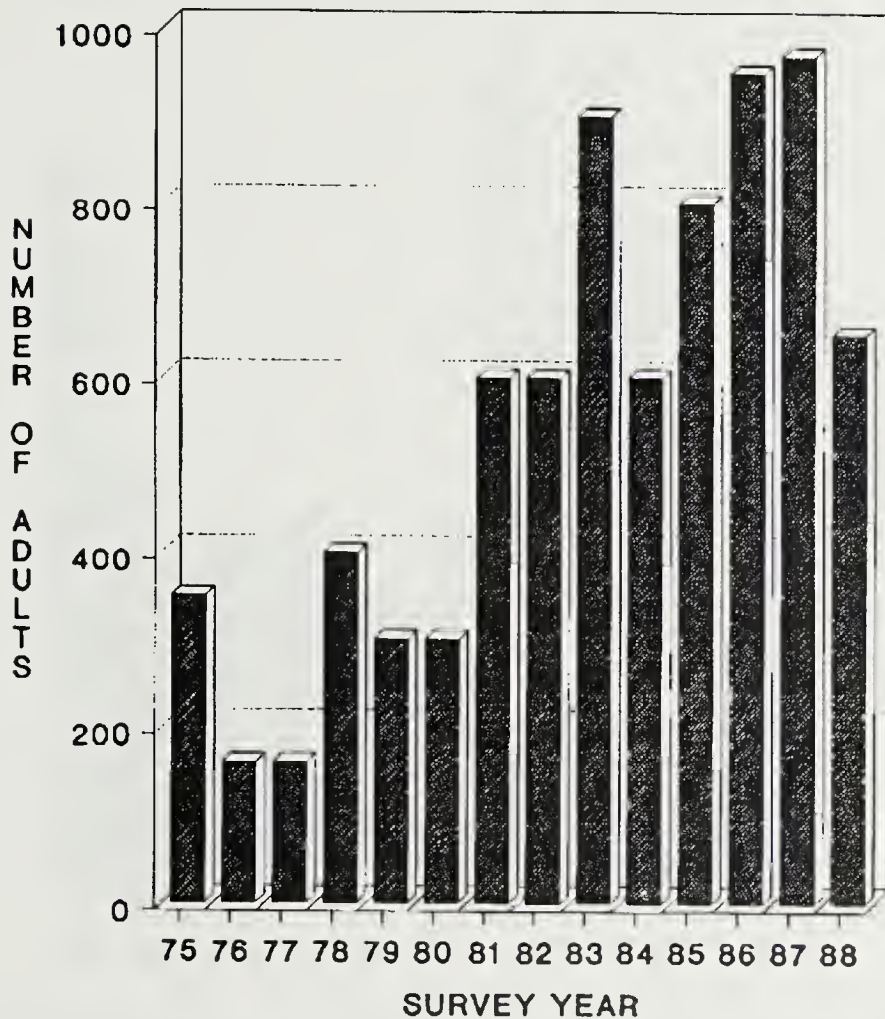


FIGURE 3. Yearly population counts of least tern adults at Grand View Beach, Hampton, Virginia.

below high tide until 1988. In 1982 a severe storm raked the islands prior to the census and resulted in the largest single-year decrease in the least tern population on the barrier islands. Population declines in 1985, 1987 and 1988 may be related to severe weather conditions during the breeding cycle.

The dynamic nature of the barrier islands has forced colonies to relocate on the same island or to abandon an island altogether. Island accretion can produce suitable tern habitat in a matter of months; erosion can destroy it in a few days. Even those islands with somewhat stable dimensions become unsuitable least tern habitat with increasing vegetation development. Establishment of gull colonies in these areas may further influence the terns. The Islands of Chimney Pole Marsh, Godwin, Mink, and Rogue are heavily vegetated with grasses and low shrubs, and no least terns have nested on these islands during the course of this study. Sandy Island, also heavily vegetated, has had only one least tern colony within this study period. Parramore Island has not been used by least terns since 1977, possibly as a result of severe storms in 1978 and 1979. Vegetation increased at the former colony site following 1979, along with mammalian and avian predation. Wreck Island is mostly covered with vegetation with areas of marginal beach habitat which have been sporadically used by least terns. Dawson Shoal has not been used as a nesting

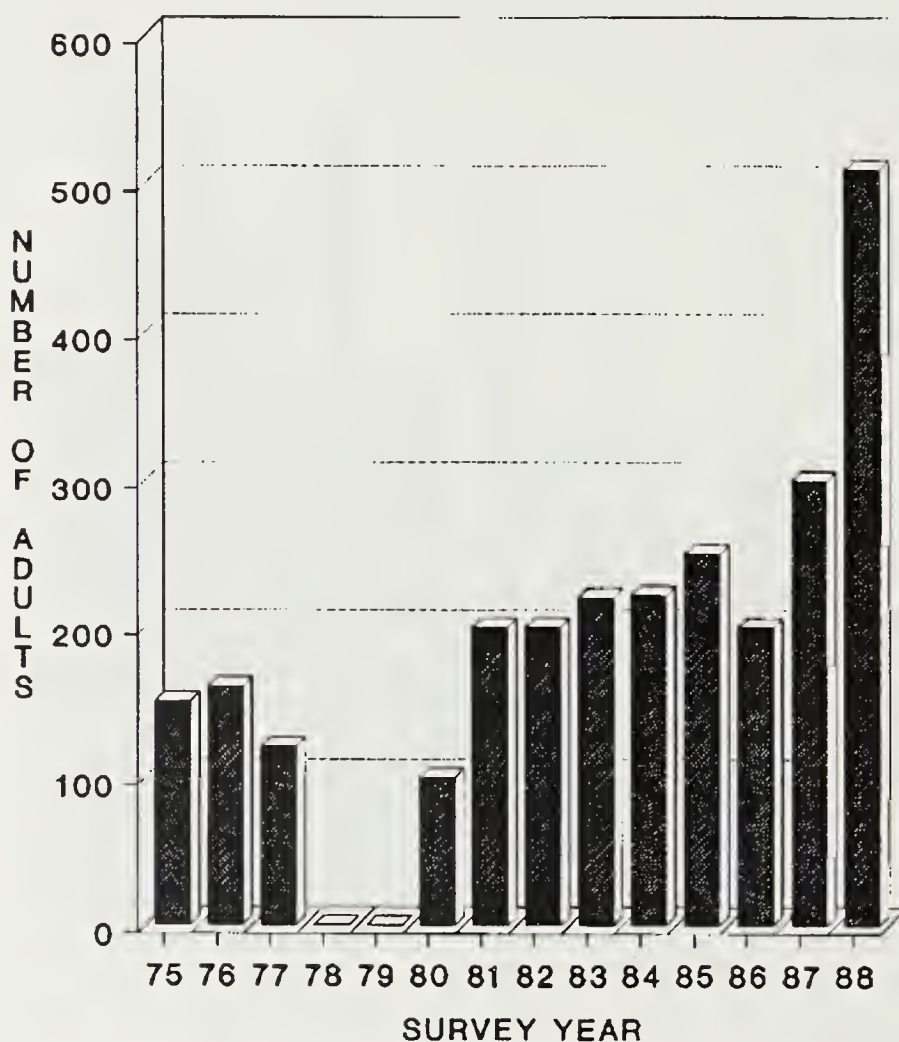


FIGURE 4. Yearly population counts of least tern adults at Craney Island, Portsmouth, Virginia.

site possibly because it is subject to frequent tidal flooding and suitable substrate is not available.

Predation on least tern colonies has been observed both directly and indirectly at all sites within Virginia. Least terns are among the most active of the Sterninae in defense of the colony. They react to predators by vocalizing, defecating, and occasionally striking at the mammalian or avian intruder. Such defensive measures are of no avail against larger mammalian predators such as red foxes (*Vulpes fulva*) and raccoons (*Procyon lotor*). Within the time period of this study, tracks and scat of both raccoons and red foxes have been documented (K. Mayne, pers. comm.), and repeated visual sightings have been made since 1986 on Metompkin and Cedar Islands. Evidence of raccoons and foxes has also been found on Assawoman Island. Parramore Island has an apparently increasing number of red foxes whose predation may have contributed to abandonment of that site by the least terns. Another, albeit rare, mammalian predator, the coyote (*Canis latrans*), has been sighted on Smith Island. This animal was first observed in 1986 and photographed in 1987 (J. Hall and B. Truitt, pers. comm.). Uncontrolled domestic dogs (*Canis familiaris*) have been observed within least tern colonies on Cedar and Metompkin Islands. No feral dogs are known to be on the barrier islands.

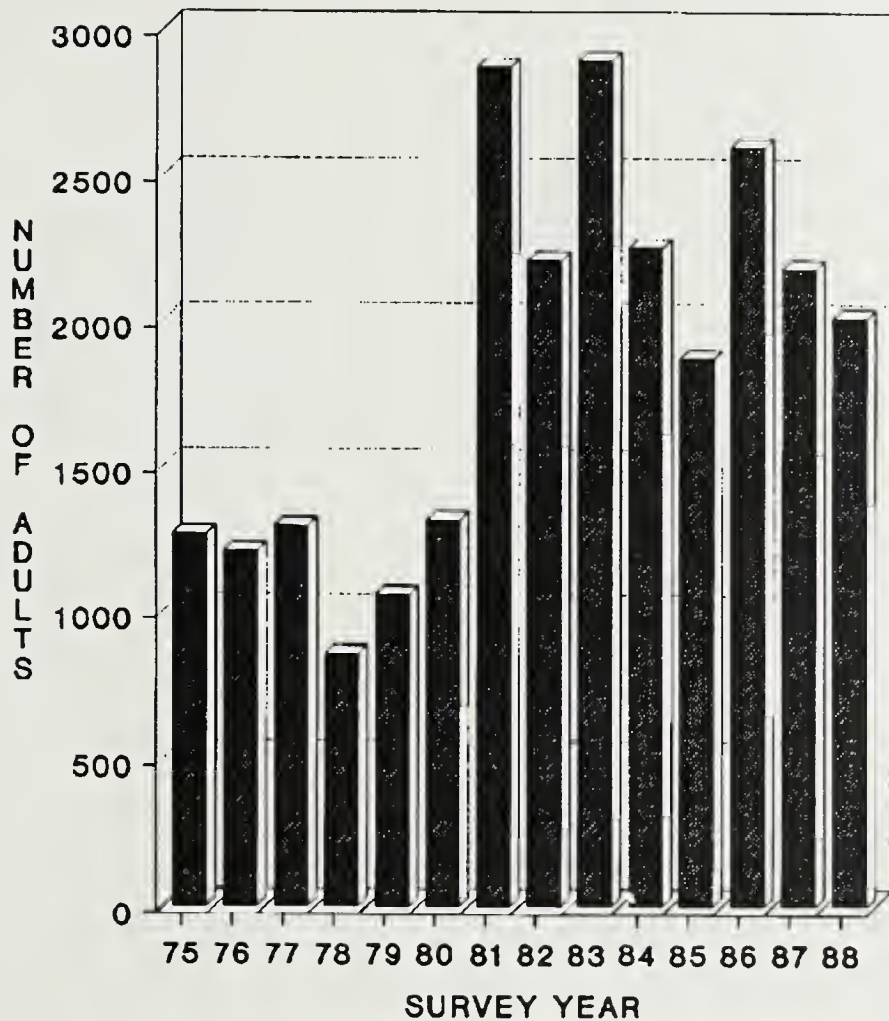


FIGURE 5. Total number of least tern adults observed in Virginia during yearly surveys from 1975 to 1988.

Avian predators include both raptors and gulls. Herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) have been observed removing chicks and eggs from least tern colonies. Raptor predators include the peregrine falcon (*Falco peregrinus*), northern harrier (*Circus cyaneus hudsonius*) and fish crow (*Corvus ossifragus*). Peregrine falcon predation of least tern adults was observed over the past six years on Metompkin Island near a hacking tower. The northern harrier has been observed in the vicinity of tern colonies at Wreck, Cobb, and Hog Islands harassing adults and taking young terns. Among these avian predators, our observations suggest that gulls represent the greater threat to a colony simply because of their large numbers and close proximity to the terns.

Feral cattle have previously been a threat to least tern colonies on Hog Island. These animals periodically wandered through colonies causing extended disturbance to the adult birds and trampling nests. The cattle were removed in 1986 under the direction of The Nature Conservancy.

Human disturbance of colonies and modifications of habitat has increased. The degree of disturbance varies from island to island. Since 1985, for example, Cedar Island has undergone substantial development including a new, larger boat dock to handle vehicles and machinery. Numerous light and heavy vehicles use the beach as the only suitable track on this island. Houses have been constructed and snow fences erected along the primary dune line. The tracks of all-terrain vehicles have

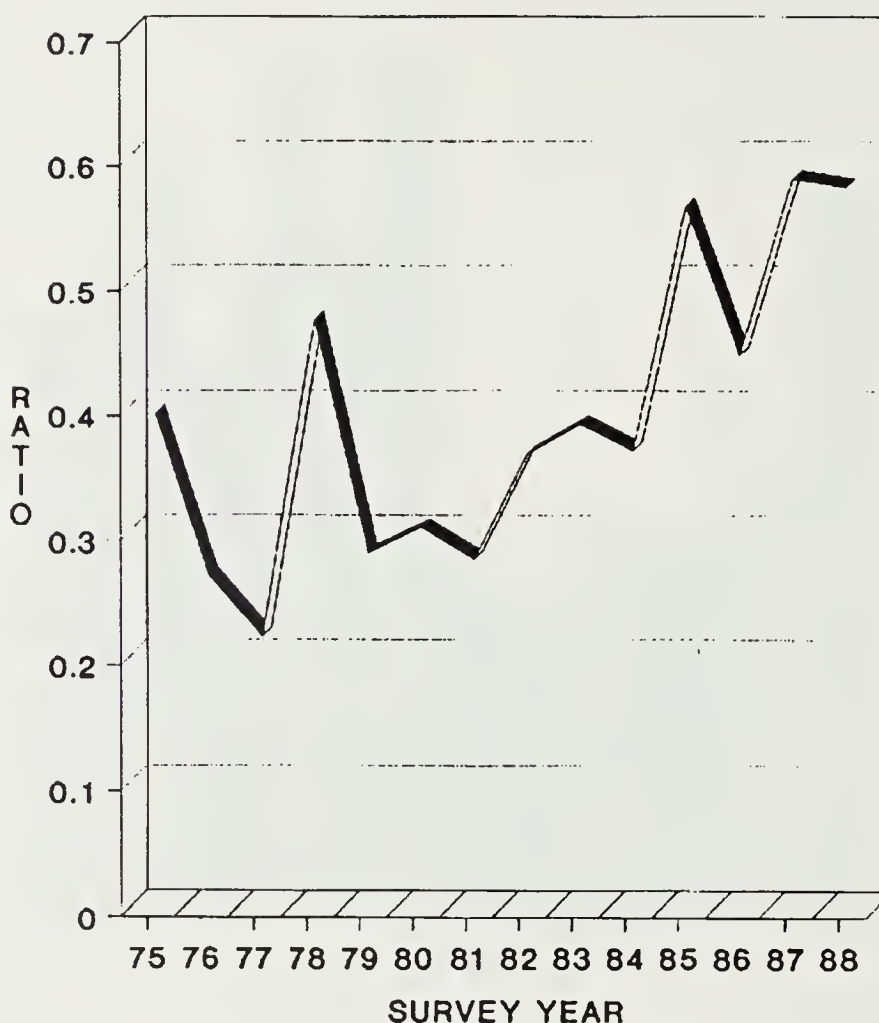


FIGURE 6. Ratio of the population of adult least terns on the west side of the Chesapeake Bay to the total Virginia population as a function of survey year.

been found crisscrossing the colonies of least terns and other beach-nesting species. Pedestrians and their dogs have been observed lounging within colonies. Least terns on other islands experience their greatest disturbance on weekends and holidays with boaters, overnight campers, and fishermen moving through the colonies or utilizing space within them. Since suitable nest site substrate for this species often occurs along island inlets, disturbance at these locations is enhanced by increased human accessibility. In the early 1980's, the boundaries of least tern colonies exposed to high human disturbance were posted with signs indicating the sensitive nature of the nesting area by the Virginia Coast Reserve of The Nature Conservancy. In addition, the Virginia Department of Game and Inland Fisheries also posts areas under its control.

Movement of breeding least terns into the colonies surveyed in this study from other areas must be considered as well as population losses to other areas. Chincoteague National Wildlife Refuge, located approximately 24 kilometers north-northeast of Assawoman Island, typically has had few least terns. In 1978, 20 adult least terns were observed on the refuge (Fig. 7). In 1979, the year with the lowest least tern count in this study, 350 were counted on the refuge. In addition, the Grand View Beach colony increased from 160 birds in 1978 to 400 in 1979. In 1982 the barrier island population showed the largest single-year decrease in this study; however, the refuge observed an increase of 854 least terns (Ailes, 1985). There

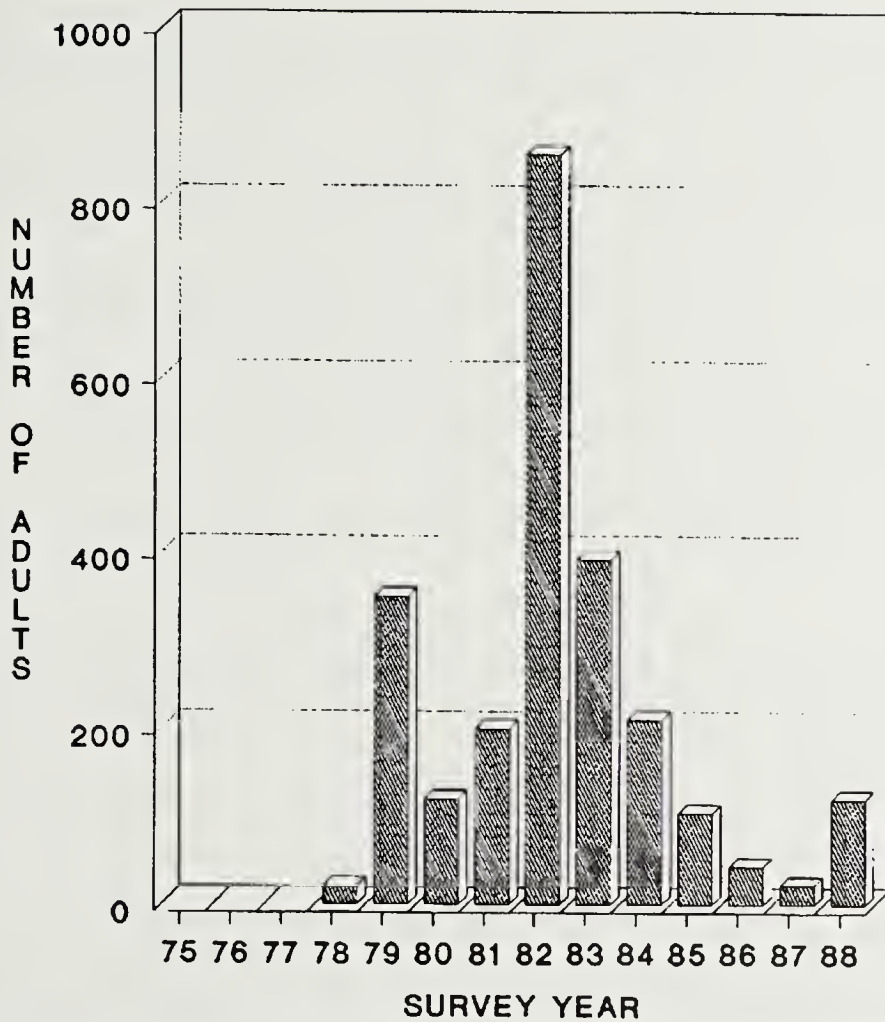


FIGURE 7. Number of adult least terns located on the Chincoteague National Wildlife Refuge from 1978 to 1988.

appears to have been a shift from the barrier islands to the west side of the Bay. However, it could be argued that the least terns normally using the barrier islands of Virginia are shifting to barrier islands of neighboring states, whereas the Craney Island and Grand View Beach colonies represent stable, growing populations. There is insufficient evidence to prove that population shifts are occurring in Virginia; however, it would seem to be an entirely plausible nesting option for this species.

A single explanation for the observed large fluctuations in numbers from year to year is perhaps not possible in view of the multiplicity of threats to the nesting environment of this species. A systematic, annual census provides only an indication of trends and potential problems and cannot address detailed questions related to natural population dynamics, predator control, and conservation strategies. The status of the least tern should continue to be monitored, and if possible, multiple surveys should be conducted each breeding season on the barrier islands to better delineate those factors which positively or adversely affect their breeding success.

Grand View Beach - This area is similar in structure to the barrier islands. It, however, escapes the worst of the storms that pound the barrier islands by virtue of its location on the west side of the Chesapeake Bay.

The least tern colony at this site dates back to (at least) 1889, when Bailey (1913) states that a large colony nested at the entrance of the Back River into the

Chesapeake Bay. The colony was destroyed by plume hunters and no information has been found concerning recolonization. A large, scattered and continuously breeding aggregation, the Grand View ternery is spread over an area of dunes that stretches southward about 300 to 350 meters from the northern tip of a small peninsula extending into the confluence of the Back River and the Chesapeake Bay. From 1975 to 1988, this colony has been among the largest in Virginia, exceeded only by the Metompkin Island colonies in 1977 and 1981.

Of the least tern young banded at Grand View, only 10 have been recovered to date. Six of these, however, were trapped as breeding adults in Dorchester County, Maryland, during 1986-87 (J. McKearnan, pers. comm.). In the absence of multiple recoveries from other locations, no significance can be attached to the Maryland recoveries in terms of population recruitment and/or shifts.

Predation by gulls does not appear to be a major problem at Grand View Beach. Gull numbers, however, continue to increase around the boundaries of the colony. Peregrine falcon predation, on the other hand, is strongly suspected with the finding of 23 adult least tern skulls, wings, and notched sternums in the 1988 breeding season. Northern harriers have been observed harassing and taking young terns at Grand View Beach. In 1987, the nest of a pair of northern harriers was found on this site (F. Day, pers. comm.).

Although evidence of predation by red foxes on Grand View Beach was observed in the early 1970's, no evidence of fox predation has been observed since the early 1980's.

Grand View Beach is public property and human disturbance of the least tern colony by boaters, picnickers, fishermen, and swimmers frequently prevented the terns from incubating eggs or caring for their young. Dogs were commonly found in the colony. In 1974, the contents of 14 nests were taken by vandals and heaped in a pile in the middle of the Grand View ternery (Akers, 1975). In an attempt to reduce the high-level human disturbance in and around the colony on Grand View Beach, two of the authors (Akers, Beck) began posting the boundaries of the colony in 1982 with the cooperation of the Hampton Department of Parks.

From 1977, this population has maintained an overall strong rate of growth. The year-to-year changes do not appear to be correlated to those of the barrier islands nor are the fluctuations as great as those of the barrier islands. However, the increasing demand for public access to this area is a continuing concern and possibly represents the greatest single threat to the long-term growth and, perhaps, survival of this colony. Continued close monitoring of this site is required and increased effort must be made to heighten public awareness of the need to protect this area as a least tern breeding site.

Craney Island - The primary avian predator at this site is the herring gull. This species has been documented removing eggs from the Craney Island site (B. Trott, pers. comm.). Immature herring gulls and great black-backed gulls have been observed walking into the colony on Craney Island.

The northern harrier has been observed in the vicinity of tern colonies at Craney Island but there has been no evidence of tern predation. The American kestrel (*Falco sparverius*), however, was observed harassing and taking young terns in 1982 and 1985.

The only known mammalian predator at this site is the red fox. In one documented case, a red fox destroyed 13 nests in a single night (Akers, 1975). At present there is no evidence to suggest that foxes are a serious threat to the terns on Craney Island.

Human activity, on the other hand, has had devastating impact on the nesting efforts at this site. In 1978 and 1979, the terns were driven from the area through extensive earth moving operations within the colony. The terns returned in 1980 and slowly increased from 200 in 1981 to 250 in 1985.

The measures taken on Craney Island with the cooperation of the Corps of Engineers have apparently resulted in a sharp increase in this population from 200 in 1986 to 510 in 1988. The current management strategy at Craney Island has the potential of becoming a model for the protection and preservation of this species at other locations. Obviously, more data are necessary before cause and effect relationships can be established.

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Piping Plover Ecology, Management, and Research Needs

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ABSTRACT

The Atlantic coast piping plover (*Charadrius melodus*) population was listed as threatened under the Endangered Species Act in January 1986 due to declining populations. Part of the decline is attributed to habitat loss from beach development and dune reclamation. Where plovers continue to nest, productivity is often low. Nest predation appears to be the most immediate threat to piping plovers in many areas. Although unrestricted recreational activity may be highly detrimental, nesting plovers can apparently habituate to some degree of human activity on beaches. Factors affecting chick mortality are not fully understood. We believe that foraging habitats have a major influence on the distribution and reproductive success of piping plovers on barrier islands. However, these hypotheses need to be tested.

Key words: barrier islands, *Charadrius melodus*, endangered species, foraging habitat, nesting habitat, piping plover, reproductive success.

INTRODUCTION

The piping plover is a migratory shorebird which breeds in the Great Lakes watershed, on the northern Great Plains of the United States and Canada, and along the Atlantic coast from Newfoundland to South Carolina (Federal Register, 1985). As a result of declining populations, plovers nesting in the Great Lakes watershed were listed as endangered and the remaining populations were listed as threatened under the Endangered Species Act in January, 1986 (Federal Register, 1985). Threats to this species include habitat loss, predation, and disturbance by humans (U.S. Fish and Wildlife Service, 1988).

Virginia and Maryland supported 16% of the known breeding population on the Atlantic Coast in 1987 (Piping Plover Recovery Team, unpubl. data). Barrier islands support 95% of the known breeding population in Virginia and the entire Maryland population (K. Terwilliger, pers. comm., Patterson, 1988). Successful piping plover management in these states requires a detailed understanding of factors affecting plover population dynamics on these islands. The following paper summarizes what is currently known about these issues, discusses management strategies, and identifies research needs.

BREEDING BIOLOGY

Piping plovers return in mid-March to Virginia and Maryland breeding grounds from wintering sites along the southern Atlantic Coast (Patterson, 1988, Haig and Oring, 1988). Courtship displays begin in March and nests may be initiated as early as mid-April (Patterson, 1988). Piping plovers almost always lay

clutches of 3 to 4 eggs (Bent, 1929; Wilcox, 1959; Cairns, 1977). Eggs are laid every other day (Wilcox, 1959; Cairns, 1982). Both male and female incubate, probably for approximately equal periods of time (Wilcox, 1959; Cairns, 1982). Incubation lasts 25 to 31 days (Wilcox, 1959; Cairns, 1982; Whyte, 1985; Haig, 1987). Although piping plovers raise only one brood per season, they have been observed reneating up to five times if nests are destroyed prior to hatch (MacIvor, 1990).

Plover chicks are precocial and young usually leave the nest within a few hours after hatch (Bent, 1929; Wilcox, 1959). Broods remain together until the chicks are able to fly, although it is not unusual for one of the adults to desert the brood within 7 to 10 days of hatch (Cairns, 1977; Whyte, 1985; Haig, 1987). Chicks grow rapidly and have been observed flying short distances 20 days after hatch (Whyte, 1985; Patterson, 1988).

Fledglings may remain on the breeding grounds longer than adults, and family groups probably do not stay together during migration (Cairns, 1977; Whyte, 1985). On Assateague Island, family groups began leaving feeding territories as early as mid-July, although one brood with 34-day old chicks was still on its feeding territory during the last week of August (Patterson, 1988).

NESTING HABITAT

Nests are shallow scrapes in the sand, usually placed well above the high tide line (Burger, 1987; Patterson, 1988). Nesting habitat is typically described as wide, sparsely vegetated beaches (Bent, 1929; Wilcox, 1959; Haig and Oring, 1987). Few studies have quantitatively analyzed vegetative cover at nest sites. As a result, it is not possible to identify the point at which vegetation cover becomes too dense for nesting. Niemi and Davis (1979) found that most plover nests occurred in areas with an average vegetative cover of 5%, but one of the ten nests they studied was placed in an area with 42% vegetative cover. On Assateague Island, most nests were located in sparsely vegetated areas, but 2 (2%) were found in areas with more than 50% vegetative cover (Patterson, 1988). Additionally, plovers on this island continue to nest on the Wild Beach in Virginia which has a narrow beach and a well established dune line. In 1987, 23 nests were located in this area.

FORAGING HABITAT

Little is known about plover foraging ecology or the role of foraging habitat in breeding site selection (U.S. Fish and Wildlife Service, 1988). On Assateague Island, piping plovers have nested in only a few specific areas for at least three years (1985-1987) (Ailes, 1985; Hoffman, 1985; Patterson, 1988). While these nesting areas were not readily distinguished by nesting habitat characteristics or human use characteristics, they did appear to be related to the location of foraging habitats (Patterson, 1988). These foraging habitats included bayside mud and sand flats, saltwater pools formed by storm tides, and a drawn-down waterfowl impoundment.

These types of foraging habitats appear to be important on other barrier islands as well. During recent surveys of barrier islands in Virginia, broods were more frequently observed on mudflats than on the high-energy beach (K. Terwilliger, pers. comm.). Fussell (1986) reported that some piping plover territories at Kathryn Jane Inlet, Cape Lookout National Seashore appeared to be closely associated with saltwater pools formed by a hurricane. Most of the other nesting pairs in this area were found on overwash or inlet flats that provided unvegetated access to the bay.

Areas that provided suitable nesting habitat, but were separated from the bay by zones of grass or shrub thickets were not utilized.

Preliminary analysis of data from Assateague Island suggests that chick survival was related to the type of foraging habitat used. On Assateague, broods foraging on bayside mud and sand flats had a higher survival rate than broods that utilized the high-energy beach. Possible explanations for this include greater prey abundance and/or quality on bayside mud and sand flats, greater human disturbance on beaches, or different predation rates.

POPULATION STATUS

Piping plover populations may have been declining since the 1930's (Arbib, 1979). The Atlantic coast population was estimated to be 910 pairs in 1979 (Cairns and McLaren, 1980). A more intensive survey was conducted along the Atlantic coast from Newfoundland to Virginia in 1987 yielding a population estimate of 745 pairs (Piping Plover Recovery Team, unpubl. data). North and South Carolina were surveyed in 1986 and had a combined total of 33 pairs (Piping Plover Recovery Team, unpubl. data). The population estimate for Virginia in 1987 was 100 pairs, and Maryland had an estimated population of 23 pairs. Plover populations on the Virginia barrier islands have been censused since 1975. The data from these surveys do not follow the national trend. Although there have been population shifts among islands, the overall population has not exhibited a decline (Williams *et al.*, 1987).

FACTORS CAUSING THE PLOVER DECLINE

Habitat loss resulting from human development of beaches is thought to be a major factor contributing to the recent population decline (Federal Register, 1985). However, little quantitative historical information summarizing actual loss of nesting habitat has been published. Wilcox (1959) described loss of former nesting areas in New York due to the construction of summer homes. Raithel (1983) suggested that the increase in summer home construction since the 1950's has reduced the amount of available plover nesting habitat in Rhode Island, and has been partially responsible for the population decline observed in the state. Increased construction has been suggested as a possible cause for the recent population decline observed on Cedar Island, Virginia (Williams *et al.*, 1987).

Dune stabilization efforts are thought to be responsible for reducing the amount of available nesting habitat by encouraging vegetation growth (Federal Register, 1985). Wilcox (1959) observed that plovers deserted one nesting area several years after dunes were rebuilt, and attributed this to the growth of vegetation. Raithel (1983) noted that plovers increase in areas which are flattened and devegetated by hurricanes and continue to increase until beaches are revegetated or dunes are rebuilt. He felt that part of the decline in suitable nesting habitat in Rhode Island is due to the lack of a destructive hurricane since 1954. Another way that dune reclamation may degrade breeding habitat is by decreasing the accessibility or availability of bayside mudflats and tidal pools.

Recreational use also may be responsible for a reduction in available breeding habitat. In Rhode Island, plovers failed to nest on Maschaug Beach for several years after ORV access was improved (C. Raithel, pers. comm.). In 1987, ORV use was no longer possible on a portion of South Beach Island, Massachusetts. During this season, several plover pairs nested in habitat which had been unavailable during

previous years due to the presence of ORV's (MacIvor, 1990). E. Strauss (pers. comm.) believed that several plover territories on Barnstable Beach, Massachusetts were abandoned prior to nest establishment due to the presence of recreationists.

However, in other areas, plovers have continued to nest despite the presence of vehicles and pedestrians. Plovers returned to Maschaug Beach five years after ORV access had been improved despite the presence of ORV's (C. Raithel, pers. comm.). Niemi and Davis (1979) found plovers nesting successfully within 10 m of frequently used roads. Strauss (pers. comm.) reported that one of the most consistently used plover territories over a five year period was exposed to heavy pedestrian and vehicular traffic. Piping plovers have been nesting on Toms Cove Hook at Chincoteague National Wildlife Refuge (Assateague Island) since at least 1978 despite heavy recreational use (Britton, 1982; Ailes, 1985; Patterson, 1988).

In Rhode Island, apparently suitable nesting habitat in the vicinity of large gull colonies is not used (Raithel, 1983). The establishment of a gull colony may be responsible for the disappearance of nesting plovers from one island in that state. Similarly, on Metompkin Island, Virginia, plovers apparently avoid a section of beach used by an expanding gull colony (Williams *et al.*, 1987).

On beaches where plovers continue to nest, productivity is often low. Cairns (1977) estimated that piping plovers on Nova Scotia beaches fledged 0-2.1 chicks/pair. Plovers on the U. S. coast in 1987 fledged 0.19-1.75 chicks/pair (Piping Plover Recovery Team, unpubl. data). Predation and recreational disturbance are usually identified as the two major factors responsible for this low reproductive success (Federal Register, 1985).

Nest predation is a problem in many areas and was the leading cause of nest loss on Assateague Island; Coast Guard Beach, Massachusetts; and Long Island, New York in 1987 (Patterson, 1988, MacIvor, 1990, D. MacLean, pers. comm.). Red foxes (*Vulpes vulpes*) were the primary predators on Coast Guard Beach and foxes and raccoons (*Procyon lotor*) were the primary predators on Assateague Island (MacIvor, 1990; Patterson, 1988). Other potential predators include opossums (*Didelphis virginiana*), skunks (*Mephitis mephitis*), domestic pets, grackles (*Quiscalus*), gulls (*Larus* spp.) and fish crows (*Corvus ossifragus*) (U.S. Fish and Wildlife Service, 1988; Patterson, 1988). The role of predation in chick mortality has not been evaluated.

Comparison of present and historic predation rates is available in only one area. During a 20-year study on Long Island, Wilcox (1959) reported that 91% of the eggs in 174 nests hatched. D. MacLean (pers. comm.) reported that at least 27% of the nests on Long Island in 1987 were lost to predators. An issue which has not been addressed is why predation appears to have increased to the point that it may be a major factor in the current population decline. It has been suggested that human activities have increased predation pressure by attracting predators to plover habitat (Federal Register, 1985; E. Strauss, pers. comm.). Also, the loss of prime nesting habitat may force plovers to nest in areas which would otherwise be avoided due to high predation pressure. Finally, the red fox may not be a natural component of some beach communities. European red foxes were introduced into New York, Maryland, and Virginia between 1650 and 1750 by fox hunters (Gilmore, 1946; Churcher, 1959). The native red fox may have been limited to northern boreal forests or the northwestern portion of the continent, and the present population in

the middle eastern U.S. may be descended from European introductions (Rhoads, 1903; Gilmore, 1946; Churcher 1959).

Human activities may reduce plover productivity directly through nest and chick destruction or indirectly by preventing birds from incubating eggs, reducing the amount of time chicks spend feeding, or attracting predators to plover nesting habitat. Many observations linking human disturbance to increased nest and chick mortality involve direct mortality: nests or chicks being crushed by cars or stepped on by people (U.S. Fish and Wildlife Service, 1988).

The indirect effects of human activities on productivity are not well understood. Although incubating plovers on isolated beaches may flush from nests when people are more than 80 m away, they can apparently become habituated to human activity nearer the nest. Cairns (1977 and Cairns and McLaren, 1980) found that some plovers on heavily used recreational beaches allowed humans to approach as close as 3 m before flushing. On a heavily used beach in Massachusetts, plovers allowed people to approach within 20 m before flushing (E. Strauss, pers. comm.). Flemming (1984) found no difference in nest success when comparing areas with different levels of recreational activity.

Cairns' (1977) study is frequently cited to indicate the adverse impacts recreational activity may have on piping plover reproductive success. She observed a fledging rate of 1.3 to 2.1 chicks/pair at Cadden Beach, Nova Scotia, while eight smaller beaches had a combined fledging rate of 0.7 to 1.1 young/pair. Cairns noted that the eight smaller beaches had much greater recreational activity than Cadden and speculated that this might be related to the difference in plover productivity. A weakness with this hypothesis is that at least two (possibly three) of the eight high human-use beaches had a fledging rate in the same range as that observed at Cadden beach. Other factors which could have contributed to the difference in productivity such as differences in predation rates or habitat quality were not evaluated. Since Cairns' study, plover nesting success at Cadden beach has plummeted, largely due to predation. In 1983, two of the eight high use beaches had a fledging rate higher than that observed on Cadden beach in 1976. One beach again had a lower fledging rate, while data for the five remaining beaches were incomplete (Flemming, 1984).

A second study from Nova Scotia is also commonly used to demonstrate the adverse impacts of recreational activity. Flemming *et al.* (1988) found that broods in areas receiving 20 or fewer recreational visits per week had higher fledging rates than broods in areas with 24 or more human visits per week. Furthermore, they reported that broods appeared to react to humans approaching within 160 m. During the first three minutes of this type of disturbance, chicks spent more time sitting and being vigilant and less time feeding and brooding than when undisturbed. ORV's did not appear to cause a major disturbance; chicks ignored or passively avoided moving vehicles.

MANAGEMENT STRATEGIES AND RESEARCH NEEDS

The national population decline and low productivity indicate that protective measures are needed now. Successful management of this species depends on application of management strategies based on the current level of knowledge combined with research designed to resolve unanswered questions.

Although a variety of factors may influence piping plover productivity, the most immediate threat in many of the existing breeding areas appears to be predation. The two primary methods to control predation are predator removal and predator exclosures. Unfocused trapping will probably not be effective. Trapping efforts should be concentrated on specific individuals immediately prior to the breeding season.

Electric fences have been used to reduce fox activity in other shorebird nesting areas (Forster, 1975; Patterson, 1977). In North Dakota, electric fences were used to protect nesting beaches adjacent to lakes (P. Mayer and M. Ryan, pers. comm.). Nest success increased, but chick survival was similar in fenced and unfenced areas. Electric fencing appeared to reduce fox predation on shorebird nests at Chincoteague National Wildlife Refuge in 1979, but was not effective during the following two years (Britton, 1982). Predator exclosures constructed around individual nests are another alternative. Experiments with killdeer (*Charadrius vociferus*) and piping plovers indicate that these birds continue to attend nests that are protected by these exclosures (Nol and Brooks, 1979; MacIvor, 1990). The exclosures around killdeer nests effectively reduced avian predation, but due to the small size, raccoons were able to reach the eggs (Nol and Brooks, 1979). Larger exclosures were used around plover nests, and preliminary experiments suggest that they may effectively reduce mammalian predation (MacIvor, 1990).

Our results from 1986 and 1987 indicate that some subpopulations experience much lower predation than others (Patterson, 1988). Studies examining predator foraging patterns are needed to determine why this is the case. It has been suggested that human presence on the beach attracts predators and increases predation rates. Although this is a plausible hypothesis, these claims are poorly documented. A specific goal of predation studies should be to determine the extent to which humans influence the activities of predators.

Very little is known about predators' contribution to chick mortality or factors which influence chick predation rates. These issues need to be addressed in greater detail.

The sensitivity of breeding plovers to human activities is an unresolved issue which warrants further investigation. On beaches where pedestrians and cars utilize the same areas as nesting plovers, recreational use clearly is a problem. However, it appears that plovers are capable of habituating to some degree of recreational activity. For example, Cairns felt that the mere presence of people probably does not affect reproductive success (Cairns and McLaren, 1980). Restricting recreational use to narrow zones immediately adjacent to the high-energy beach using symbolic fencing may effectively eliminate significant disturbance to plovers nesting on some wide beaches. During a four year study at Chincoteague National Wildlife Refuge, none of the shorebird nests protected by symbolic fencing were lost to direct human disturbance (Britton, 1982). In 1987, the only nest loss on the refuge attributed directly to human destruction occurred outside of the symbolic fence (Patterson, 1988).

A major unanswered question is how recreational activity influences chick survival. The answer may differ among beaches depending on the location of brood foraging areas. Broods feeding on the high-energy beach may be highly sensitive to recreational use, while broods foraging on bayside flats may not be significantly

disturbed or may be adequately protected by the same fencing used to prevent destruction of nests.

A large gap in our understanding of piping plover ecology is the absence of data about diet and foraging habits. We believe that foraging habitat is important in nest site selection on barrier islands and that it is a major factor in chick survival. Additionally, because foraging habitat seems to regulate nest placement, it may also influence predation rates. However, these hypotheses have not been tested. These issues need to be addressed to refine the ability to identify potential breeding habitat, to enhance efforts to improve existing habitat, and to improve efforts to create additional habitat.

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Phytoplankton Within the Virginia Barrier Island Complex

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ABSTRACT

Phytoplankton populations within channels of the Virginia barrier islands are characterized as neritic and similar in dominant species, general composition and seasonal growth patterns to populations of the coastal waters in the mid-Atlantic bight. Differences in composition increase along a decreasing salinity gradient when compared to populations in a saline pond and an oligohaline lake.

Key words: Phytoplankton, Barrier Islands, Virginia

INTRODUCTION

Phytoplankton represent the major autotrophic component within marine and most estuarine habitats. One of the more dynamic and unique assortments of habitats for phytoplankton development is present in the Virginia barrier islands complex. Behind the seaward band of barrier islands are numerous low elevation islands consisting of nothing more than tidal wetlands and mud flats. These wetlands contain numerous channels of natural origin and varied depth that are tidally flushed daily, with the bordering wetlands inundated during spring tides and major storm periods. Numerous deep inlets between the barrier islands connect these inner waterways to the ocean and provide direct exchange passage for waters entering and leaving this area. The region provides a high energy system, where the water masses are continually being transferred and are well-mixed, oxygenized, and exposed to nutrient rich drainage from upland and wetlands sites. Plankton and other biota are continually brought to the area from coastal waters and are flushed out again. The phytoplankton in these waterways may come from offshore, the wetlands, or upland drainage from the islands or mainland. The purpose of this paper is to characterize the phytoplankton composition within the barrier island complex and compare the seasonal dominants and growth patterns from several of these habitats.

COASTAL PHYTOPLANKTON

The phytoplankton in the offshore waters of the Barrier Islands between Cape Henry, Virginia and Cape May, New Jersey have been identified by Marshall and Cohn (1987a). They identified 103 taxa for this region, with the near shore flora composed mainly of chain-forming diatoms, dinoflagellates, and picoplankton. This last category was dominated by cyanobacteria less than 3 microns in size. There were numerous diatom pulses during the year, sometimes several per season, with *Skeletonema costatum*, *Leptocylindrus minimus*, *Thalassiosira nordenskioldii*, and *Asterionella glacialis* common and abundant. The spring bloom typically followed an early winter low, with rapid growth beginning in late winter and reaching peak development in early spring. A late fall growth often

blends into the spring bloom during mild winter conditions. Late spring and summer populations generally changed to a different diatom assemblage of *Cerataulina pelagica*, *Guinardia flaccida*, *Leptocylindrus danicus*, and several *Chaetoceros* spp. The abundant dinoflagellates included *Prorocentrum minimum*, *P. micans*, *Ceratium fusus*, *C. lineatum* and *C. tripos*. Also common in coastal waters were cryptomonads, euglenoids and chrysophytes. The chrysophytes included several silicoflagellates (*Dityocha fibula*, *Distephanus speculum*), plus *Calycomonas ovalis* and *C. gracilis*. In general, the phytoplankton is similar to that found in coastal waters along the entire mid-Atlantic bight (Marshall and Cohn, 1987a, b).

Although the phytoplankton composition is similar along the mid-Atlantic bight, there are differences in cell concentrations. Marshall and Cohn (1987a) reported a decline in abundance from New York Bay southward to Chesapeake Bay, although a slight increase in concentrations appears associated with the Delaware Bay plume. In general, this region is situated between more productive areas of the New York Bight and those south of the Chesapeake Bay entrance. The Delaware Bay plume enhances cell concentrations in the vicinity of Cape May and toward the barrier islands, but a major increase in abundance is not found until south of the Chesapeake Bay. Phytoplankton from the Delaware plume is also similar to the coastal waters of the shelf. In the barrier islands, the inner channels are connected to numerous inlets between the barrier islands that allow coastal waters to enter the channels and transport predominantly marine phytoplankton comparable to the Delaware Bay and local shelf waters into this complex.

CHANNEL PHYTOPLANKTON

A characteristic neritic phytoplankton flora similar to populations in the mid-Atlantic bight are consistently found within the barrier island channels. Salinity within these channels is typically between 25 and 33 ‰. Marshall *et al.*, (1981) identified 192 species in these channels, with seasonal dominants the same as those noted over the shelf. However, many of the average cell concentrations were greater within the channels than reported for the coastal waters. For instance, Marshall and Cohn (1987a) found the annual mean concentration of the dominant *Skeletonema costatum* to be 37×10^2 cells/l in the coastal waters. Marshall *et al.*, (1981) found that it reached bloom status (1.95×10^6) in the barrier island channels. For comparison, *S. costatum* averaged 556×10^3 cells/l in the Chesapeake Bay plume (Marshall and Lacouture, 1987).

Unfortunately, there are little data on comparable seasonal samples from channels and offshore waters. However, there is a nine-month overlap between the channel collections of 1978-1979 by Marshall *et al.* (1981) and the collections in coastal waters from 12 cruises between 1979 and 1981 by Marshall and Cohn (1987a). The channels had a spring pulse in January and a larger development in March 1979, when average cell counts reached 1.89×10^6 cells/l. There was a decline into early summer, followed by a more modest pulse in late summer, with lowest mean concentrations in winter (1.7×10^5 cells/l). Mean cell concentrations offshore from the barrier islands ranged from 10^5 to 10^7 cells/l during the spring months. In addition, the seasonal periods contained the same dominants as in the channels. The average offshore spring pulse occurred by February, declined from mid-spring to summer, before it increased again by late summer or early fall. Of

interest was the increased representation of cyanobacteria within the channels in comparison with adjacent offshore waters. These included a variety of colonial and filamentous forms that may have originated from the wetlands marshes of this region and daily seeded the tidal and offshore waters. Higher concentrations of pennate diatoms, associated with the benthos and mud algae, were also found in the channels. However, there were also numerous chlorophycean, cyanophycean and euglenophycean species reported in the tidal creeks of the nearby mainland by Nemeth (1969) that were not observed in the channels.

Nesius *et al.* (1983) reported on primary production within the barrier island channels. Monthly production rates followed a seasonal pattern, being lowest in winter and highest in summer. The annual production rate in these channels was $178 \text{ g C/m}^2/\text{yr}$. Rates ranged from winter lows of approximately $1 \text{ mg C/m}^2/\text{hr}$ (February) to a summer high of $290 \text{ mg C/m}^2/\text{hr}$ in June. In comparison, O'Reilly and Busch (1987) reported the productivity rate of offshore waters east of the barrier islands as $360 \text{ g C/m}^2/\text{yr}$. Other east coast estuaries show a wide range of productivity rates. These include: $53\text{-}67 \text{ g C/m}^2/\text{yr}$ in Beaufort N.C. (Williams, 1966) to $546 \text{ g C/m}^2/\text{yr}$ in the Allamaha River in Georgia (Thomas, 1966). Sellner *et al.* (1976) reported annual phytoplankton production at North Inlet, South Carolina as 346 g C/m^2 . These comparisons indicate the channels of the barrier islands to be productive, but with annual rates less than what has been reported in the nearby coastal waters and in several of the more productive estuaries on the east coast.

POND AND LAKE PHYTOPLANKTON

Ponds of various sizes are common on the barrier islands. The larger islands have elevations capable of supporting permanent stands of water. Many of the ponds are temporary and associated with periods of increased rainfall in late winter and spring. After major storms, small lagoons are also common in interior swales, but generally these have a short period of existence. The largest concentration of standing water is Goose Lake on Parramore Island, with an area of 0.07 km^2 (Marshall, 1980). Parramore is approximately $13.3 \times 3 \text{ km}$ in size, with its long axis oriented in a general northeast direction. The island's topography decreases in elevation along the southern and western margin where an extensive wetland has developed. The elevation of the island changes dramatically along an east-west transect because there are a series of raised relict dunes (up to 9.1 m above mean low water) separated by areas of lesser elevation. It is within one of these lowland areas that Goose Lake was formed. It is oligohaline (less than 5 ‰), but subject to higher salinities under storm conditions. At this time salt water frequently floods the southern lowlands and may enter Goose Lake. Under such conditions in October 1978 Goose Lake salinity averaged 20 ‰ .

Marshall (1980) reported 154 phytoplankton species in Goose Lake with diatoms and chlorophyceans the most diversified and abundant groups. There were summer and fall maxima in cell concentrations with lowest numbers in winter. The average abundance during a June (summer) pulse was $1.5 \times 10^6 \text{ cells/l}$. In winter the phytoplankton was characterized by pennate diatoms and chlorophyceans, but both pennate and centric diatoms were dominant in spring. The composition changed in summer to mainly centric diatoms and cyanobacteria.

The fall assemblage was dominated by centric diatoms, cryptomonads, euglenoids and chlorophyceans. The common centrics were *Cyclotella striata*, *C. caspia* and *C. meneghiniana*. In general, the lake contained both freshwater and marine flora. The marine flora composition was enriched after periods of storm flooding. The freshwater flora became more abundant and diversified after periods of precipitation which lowered salinity values. Ubiquitous in Goose Lake throughout the seasons was a pico- nanoplankton component of unidentified cyanobacteria.

The phytoplankton in a permanent saline pond on Smith Island was reported by Marshall (1983). Located between Fisherman and Myrtle Islands, Smith Island is approximately 12 km in length and 0.85 km wide. It consists of a series of parallel ridges separated by swales, some containing salt marsh and small ponds. The saline pond studied is approximately 80 x 1.5 - 3.5 meters in size, with a maximum depth of 0.6 m. It is surrounded by salt marsh vegetation and has an annual salinity that ranged from 12 to 30 ‰. There were 146 species identified for this pond, plus a pico-nanoplankton component (less than 3 microns in size) that represented the most abundant cells in the samples. Diatoms and chlorophyceans were numerous and dominated by estuarine and marine species, and several freshwater species in low concentrations. Also common were the euryhaline species that included the diatoms *Cyclotella caspia*, *C. glomerata*, *C. meneghiniana* and *Melosira distans*. There was a diversified assemblage of cyanobacteria including filamentous (*Oscillatoria* spp.) and colonial (*Anacystis* spp.) forms.

There is a direct relationship between the percentage of the species which occur at a site and its salinity, with the salinity decreasing from the shelf into the channels and less from the saline pond to Goose Lake. For instance, 56% of the shelf species were in the inner channels, 22% in the Smith Island pond, and 13% in Goose Lake (Table 1). In contrast, 38% of the species noted in oligohaline Goose Lake were in the Smith Island pond, 17% in the channels, and 9% in shelf waters.

DISCUSSION

The barrier islands complex offers a variety of habitats for phytoplankton development. Atlantic coastal waters border the eastern margin of the islands, with the western flank exposed to an array of channels and wetland islands that extend westward to the mainland. Small bodies of standing water with abundant phytoplankton are common on the barrier islands, with the largest inland water body being Goose Lake on Parramore Island. More stable environmental conditions and consistent floral composition are associated with the coastal and channel waters surrounding these islands, in contrast to the temporary and permanent ponds which are subject to more severe and changing environmental conditions. These events would include storm induced flooding, salt spray, severe temperature and salinity ranges, and variable rainfall and evaporation patterns. Due to these changes there are greater fluctuations in different phytoplankton population abundance and composition within these ponds. For instance, it was not uncommon to find summer blooms of phytoplankton in one pond but not in ponds located nearby. The variation and extremes in salinity, temperature, and nutrients influence the different taxa within the ponds either favorably or not favorably, and these changes in abundance and composition are not necessarily repeated annually or similarly

TABLE 1. Phytoplankton species overlap among four sites in the Virginia barrier islands. Numbers represent the percent of the total number that are shared between sites.

| SITES | Goose Lake | Smith Pond | Channels | Shelf |
|------------|------------|------------|----------|-------|
| GOOSE LAKE | - | 38 | 17 | 9 |
| SMITH POND | 40 | - | 28 | 17 |
| CHANNELS | 16 | 23 | - | 30 |
| SHELF | 13 | 22 | 56 | - |

in different standing waters. Each pond represents a unique habitat, with the floral expression an indication of the degree of differences between those sites and the waters they contain. In contrast, the phytoplankton in the channels of the barrier islands complex are characterized as neritic flora, most similar in composition and development to species of the inner shelf waters of the mid-Atlantic bight. Many of neritic species decline in their number, abundance, and degree of expression in local lower salinity habitats. Conversely, there is a similar reduction in the presence and expression of species from oligohaline sites to those of increased salinity. However, there is continued interaction of floral transport and presence between these areas. Phytoplankton entry into the channels is enhanced by the daily tidal flushing and local storms. Land or island-derived populations do not represent a significant source of channel species. However, the extensive mud flats and benthic substrate within the wetlands provide a seeding source for a variety of cyanobacteria and mud algae (e.g., pennate diatoms) that are common in channel waters.

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Marine Amoebae in Waters of Chincoteague Bay, Virginia: Ecological Significance of "Old" and "New" Species.

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ABSTRACT

Surface waters from Chincoteague Bay, Virginia, were sampled for marine amoebae in 1971-72. Seawater cultures yielded four new genera and 20 new species in addition to 16 genera and 15 species of previously described marine amoebae. Among the 16 "older" genera, six were described during 1874-1912, six during 1921-31, and four during 1950-72. The description of 20 new species in 1975 indicated that marine amoebae had not received adequate attention as important components of marine ecosystems. Several of the "new" species are now recognized as indicators of healthy or stressed environments. Similarly, the "old" genus *Paramoeba* Schaudinn, 1896 now includes a parasitic species that causes fatal disease in blue crabs, *Callinectes sapidus*, and *Acanthamoeba* Volkonsky, 1931 includes several that may cause meningitis or blindness in humans. Coastal waters of Virginia are known to harbor free-living pathogenic amoebae that deserve further ecological and taxonomic study, especially in marshlands, tidal creeks, and rivers.

Key Words: protozoa, marine amoebae, Chincoteague Bay

INTRODUCTION

Naked marine amoebae are unicellular animals (Protozoa) classified taxonomically in the same group (Sarcodina) as the radiolaria, heliozoa, and foraminifera. In contrast to most of the other groups of protozoa, amoebae are devoid of visible scales or tests that provide fixed or persistent morphological features that aid in their identification. Most amoebae have distinct shapes while in locomotion and possess distinct types of pseudopods that assist in placing them in broad taxonomic groupings at least to the family level. Although many species of freshwater and soil amoebae have cyst stages that are useful in identifying them, marine species rarely, if ever, undergo encystment. Identifications to species often require studies on stained specimens to determine types of nuclear division, culture in dilute seawater media to determine salinity tolerance, and/or studies with the electron microscope.

Prior to the 1900's there were approximately 12 well-described species of marine amoebae and 11 others placed within rather loosely defined genera. Schaeffer (1926) published the first monograph to place a diverse group of freshwater and marine species into well-described genera and families. His descriptions were based on patterns of locomotion, types of pseudopods, crystalline inclusions, food habits, etc. He also conducted salinity tolerance tests and found that none of the

marine species could be cultured continuously in freshwater. Bovee (1950, 1953) extended the work of Schaeffer (1926) and established many new genera and species. Bovee (1953) published an excellent account of the various morphological features useful for identifying free-living amoebae. Bovee and Sawyer (1979) and Page (1983) have published keys to the identification of marine amoebae.

Studies on marine amoebae presented here were carried out by culturing species from the surface waters of Chincoteague Bay, Virginia, near Franklin City during the period January 1971 - January 1972. The discovery of four new genera and 20 new species in Virginia waters (Sawyer, 1975a,b,c,) brought the total of well-described marine species to approximately 84 (Bovee and Sawyer, 1979). The project was designed to provide an historical database on the diversity of amoebae readily cultured from reasonably clean or unpolluted coastal waters. Results of the project were published to provide a basis for future studies on environmental quality as land and water use continue to impact on the Bay.

METHODS

Water from Chincoteague Bay was sampled by floating sterile 1 liter bottles on the surface until they became half-filled and began to sink. String attached to the bottle necks was used to hold them in an upright position and prevent them from sinking below the surface. Samples were filtered through $1.2\ \mu$ filters under weak vacuum until a thin layer of water remained on the surface. Filters were inverted and floated overnight on the surface of filtered water placed in sterile 60 mm plastic culture dishes. Filters were removed and each dish examined with an inverted Leitz microscope to note the presence of amoebae, ciliates, diatoms, *etc.* Water from each dish was removed with a sterile fine-tipped pipette leaving approximately 1 ml in the dish, and placed in sterile test-tubes. Water remaining in each dish was used to flush the bottom and 2-3 drops were placed on agar plates streaked with bacteria (*Klebsiella aerogenes*). Original cultures were re-established by returning the water from the test-tubes to the appropriate plate. Agar media were prepared by melting 15g Difco agar, 0.1g yeast extract, and 0.1g malt extract in seawater (20-24 o/oo) sterilized by autoclaving. Culture methods, staining procedures, and methods used for identifications are as published earlier (Sawyer, 1975a; Bovee and Sawyer, 1979; Sawyer and Bodammer, 1982).

RESULTS

Microscopic studies on 185 strains of marine amoebae showed that 30 of them, culturable on semi-moist agar plates, and five that would grow only with a seawater overlay, were distinct species assignable to 20 genera (Sawyer, 1973). Four genera and 15 species (20 strains), did not have the features of any adequately described species and were described as new to science (Sawyer, 1975a,b,c). Seven of the recognized genera (Table 1), *i.e.*, *Hyalodiscus*, *Saccamoeba*, *Thecamoeba*, *Paramoeba*, *Vahlkampfia*, *Pelomyxa*, and *Acanthamoeba*, were described prior to Schaeffer's 1926 monograph. Five others (Table 1) were described by Schaeffer, *i.e.*, *Mayorella*, *Unda*, *Gibbodiscus*, *Vexillifera*, *Flabellula*; two by Bovee, *Vannella*, *Triaenamoeba*, and two by Page, *Platyamoeba*, and *Rhizamoeba*. The four newly described genera were *Clydonella*, *Lingulamoeba*, *Boveela*, and *Stygamoeba* (Table 1). All of the amoebae were recovered from waters that did not exceed 2m deep. Among the 20 new species, eight were $20\ \mu$ or less in greatest dimension, seven

TABLE 1. Distribution of marine amoebae in coastal waters of the northeastern United States (partial listing).

| Genus | Chincoteague ¹ Bay | Chincoteague ² Bay | Sandy Hook ² New Jersey | WoodsHole ² Massachusetts |
|-----------------------------|----------------------------------|----------------------------------|---------------------------------------|---|
| <i>Flabellula</i> | + | + | + | + |
| <i>Platyamoeba</i> | + | + | + | + |
| <i>Thecamoeba</i> | + | + | + | + |
| <i>Pelomyxa</i> | + | + | + | - |
| <i>Clydonella</i> | + | + | - | + |
| <i>Mayorella</i> | + | + | - | + |
| <i>Paramoeba</i> | + | - | - | - |
| <i>Boveela</i> | + | - | - | - |
| <i>Stygamoeba</i> | + | - | - | - |
| <i>Vannella</i> | + | + | - | + |
| <i>Acanthamoeba</i> | + | + | - | - |
| <i>Lingulamoeba</i> | + | - | - | + |
| <i>Triaenamoeba</i> | + | - | - | - |
| <i>Vexillifera</i> | + | - | - | - |
| <i>Gibbodiscus</i> | + | - | - | - |
| <i>Vahlkampfia</i> | + | + | + | + |
| <i>Unda</i> | + | - | - | + |
| <i>Saccamoeba</i> | + | + | + | + |
| <i>Hyalodiscus</i> | + | - | - | - |
| <i>Rhizamoeba</i> | + | - | - | - |
| Genera present ³ | 20/20 | 10/20 | 6/20 | 10/20 |

¹From Sawyer, 1975a,b,c²Bovee, E.C. (Personal communication)³Numerator = no. genera identified per location/Denominator = Total no. genera identified.

measured over 20 but less than 30 μ , 11 measured between 30 and 40 μ , and only one *Mayorella corlissi*, measured up to 100 μ .

DISCUSSION

The Chincoteague Bay studies yielded the first comprehensive account of marine amoebae in Virginia coastal waters. The discovery of 20 new species illustrated the very limited knowledge on species diversity among naked sarcodines in estuarine waters of the northeastern U.S. Recent interest in amoebae as important components of marine waters and sediments (Sawyer, 1980) have shown that several genera, including *Paramoeba*, *Platyamoeba*, and *Clydonella* probably are cosmopolitan in saline waters. Species of *Acanthamoeba* are also common in coastal and ocean sediments contaminated with sewage wastes (Sawyer, 1980; O'Malley *et al.*, 1982; Sawyer *et al.*, 1982). Taxonomic studies have shown that careful microscopic studies on seemingly unimportant or transient features of marine amoebae are often the definitive characteristics for identifying these protozoa (Schaeffer, 1926; Bovee, 1953; Bovee and Sawyer, 1979; Page, 1983).

Follow-up studies in Chincoteague Bay should benefit from the historical findings reported here and possibly provide useful information on changes in species diversity that may have occurred during the past two decades.

Significance of "Old" Genera & Species - The genus *Hyalodiscus* Hertwig & Lesser, 1874 has not been studied adequately since its original description. Although valid, the genus would require complete revision should the type species be found in future studies. *Thecamoeba* Fromentel, 1874 is a well-described genus and now accommodates a variety of freshwater and marine species that are readily identified with existing keys. *Paramoeba* Schaudinn, 1896 was the only genus to be proposed for an exclusively marine species prior to 1900. Species assigned to *Paramoeba* may bear superficial resemblance to species of *Mayorella* Schaeffer, 1926 and *Vexillifera* Schaeffer, 1926, but differ by having a stainable inclusion near the nucleus. The inclusion has been called a secondary body, Nebenkörper, amphosome, parasome, etc. The genus *Paramoeba* includes *P. perniciosa* Sprague, Beckett, & Sawyer, 1969, parasitic in the blue crab, *Callinectes sapidus*. Sawyer (1976) reported a parasitic amoeba from histologic sections of the American lobster, *Homarus americanus*, and the rock crab, *Cancer irroratus*, that was identical to *P. perniciosa* as seen in sections of the blue crab. The genus *Vahlkampfia* Chatton & LaLung-Bonnaire, 1912 was established to accommodate an amoeba isolated from a diarrheic stool of a hospitalized patient. The genus now includes a variety of soil, freshwater, and marine amoebae. All species within this genus have a mitotic pattern where the nuclear membrane and nucleolus persist throughout the division process. All of the "old" genera accommodate species of amoebae that are important in the marine food web feeding upon bacteria, other protozoa, diatoms, etc. Some species that are recognized as obligate or opportunistic pathogens are important in the health of plant and animal life in nature and in aquaculture systems.

Significance of "New" Genera & Species - Most of the marine amoebae described since 1926 were studied from pure clonal cultures thereby eliminating descriptions that may have been based on mixed populations. Many of the species recognized prior to 1926 have been re-described from clonal cultures using phase-contrast microscopy, staining techniques, and scanning and transmission electron microscopy (Page, 1983). Recent interest in marine pollution, nutrient recycling in marine food webs, taxonomy, systematics, and diseases of marine animals have shown that amoebae, in addition to well-known flagellates and ciliates, are more important than previously recognized. Most of the amoebae that are frequently cultured from surface waters feed almost exclusively on bacteria, and others probably on microalgae and flagellates. *Platyamoeba* Page, 1969, *Clydonella* Sawyer, 1975, *Vannella* Bovee, 1965, and several small species of *Paramoeba* Schaudinn, 1896, are common in marine surface waters and feed extensively on bacteria. Munson (1988) routinely found *Paramoeba*, *Platyamoeba*, *Clydonella*, *Vannella*, and *Hartmannella* in surface waters 10 and 33 km. off of Sapelo Island, Georgia. Larger amoebae, e. g., *Mayorella*, *Vexillifera*, *Thecamoeba*, *Hyalodiscus*, and *Unda* have been found primarily in shallow coastal waters and marshes where they may feed upon algae and diatoms, as well as bacteria. The relative ease of identifying most of the "new" species was estimated by Bovee (personal communication). He studied amoebae from surface water, tidal pools, and salt marshes at

Chincoteague Bay, Sandy Hook, New Jersey, and Woods Hole, Massachusetts. Bovee found 11 of the "new" species in Chincoteague waters, two at Sandy Hook, and seven at Woods Hole. He considered the Chincoteague ecosystem to be relatively clean, Woods Hole moderately polluted, and Sandy Hook as highly polluted. Bovee's unpublished findings agreed with his estimates of ecosystem quality, *i. e.*, 13 genera and 27 species from clean waters, 10 genera and 27 species from moderately polluted waters, and seven genera and 19 species from highly polluted waters. The distribution of genera shown in Table 1 suggests that new studies are desirable to support the generally accepted belief that protozoan diversity attains a maximum only in clean unpolluted ecosystems. Previous studies (Sawyer, 1980) indicated that small bacterivorous species adapt to changes in water quality, however, very little is known about factors that influence the presence or absence of larger shoreline or salt marsh species.

Progress in Understanding the Pathogenic Potential of Marine Amoebae - Chatton (1910) published one of the earliest reports of marine amoebae (*Vahlkampfia*) as being associated with fish mortalities. He noted mortalities in aquaria fish and found massive numbers of amoebae (*Vahlkampfia mucicola*) covering the gills and probably causing respiratory stress. Hogue (1914) found two new species of *Flabellulla* in the gut contents of oysters, *Crassostrea virginica* (originally placed in the genus *Vahlkampfia*). Later, *Thecamoeba hoffmani* was described from gills of fingerling fish (Sawyer *et al.*, 1975) and *Pseudovahlkampfia emersoni* was described from the gills of rock crabs, *C. irroratus*, and the intestinal contents of blue crabs, *C. sapidus* (Sawyer, 1980). *Paramoeba pemaquidensis* Page, 1970, a well-known free-living amoeba, was recently reported from the gills of dead or dying Coho salmon, *Oncorhynchus kisutch* reared in aquaculture facilities (Kent, *et al.*, 1988). Thus, marine amoebae, as well as other groups of protozoa, may be involved with stress in marine animals to a greater extent than presently appreciated. Sick or dying animals usually are dissected and their tissues examined for microorganisms in histologic sections. Gill-fouling microorganisms are often lost or reduced in numbers subsequent to fixation, processing, sectioning, and staining. Mortalities among marine fish and crustacea, regardless of the cause, are difficult to assess since weakened or stressed animals are readily consumed by predators.

Salinity tests showed that only one strain of euryhaline amoeba was recovered from surface waters of the Bay. The amoeba, although not identified to species, formed resistant wrinkled cysts characteristic of the genus *Acanthamoeba*. Several species belonging to this genus are known to grow at mammalian body temperatures and cause fatal amoebic meningitis in humans and experimental animals (Martinez, 1985). Other species of *Acanthamoeba* that do not grow at elevated temperatures have been cultured and identified from patients with eye disease (Morbidity and Mortality Weekly Report, 1986). Several years after the Chincoteague Bay studies, it was learned that both pathogenic and non-pathogenic species of *Acanthamoeba* may be cultured from sewage-contaminated marine sediments when distilled water or low salinity seawater (3-5 o/oo) are used in preparing the agar media (Sawyer *et al.*, 1977; Sawyer *et al.*, 1982; Daggett *et al.*, 1982). Today it is recognized that certain cyst-forming soil amoebae (*Acanthamoeba*, *Hartmannella*, *Vahlkampfia*), although

not classified as marine amoebae, serve as excellent indicators of sewage or thermal pollution in fresh, brackish, and marine ecosystems.

CONCLUSIONS

Modern taxonomic keys to marine amoebae by Bovee and Sawyer (1979) list approximately 34 genera and 84 species, and by Page (1983), 31 genera and 81 species. Further studies undoubtedly will add many other new species to this growing list and contribute to redescriptions of some that are of uncertain taxonomic status. Page (1983) lists 14 species assigned within the genera *Amoeba* or *Amiba*, described between 1841-1963 (10 prior to 1900) that require further taxonomic study. Among the 84 species listed by Bovee and Sawyer (1979), 20 were first isolated from Chincoteague Bay, inland near Franklin City. Further studies on open waters, vegetated shorelines, and bottom sediments would be likely to yield other new species, especially larger ones that feed on diatoms, algae, blue green algae, and other microorganisms. Other studies on sewage-associated bacteria and freshwater or soil (anthropomorphic) cyst-forming amoebae could provide new information on the present status of sewage pollution resulting from increasing recreational, residential, and commercial land and water use. Sawyer and Munson (1988) made a preliminary study on cyst-forming amoebae in shoreline and inland sediments at Sapelo Island, Georgia and identified 10 species of *Acanthamoeba*, including several that are well-known pathogens. Historical data on species diversity among marine amoebae during 1971-1972 should provide a useful historical record for developing a water quality model for the shoreline of Chincoteague Bay as it undergoes further development.

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Seasonal Composition of Finfish in Waters Behind the Virginia Barrier Islands

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ABSTRACT

Semi-monthly sampling of finfish was conducted in the lagoons and marshes behind Parramore and Cedar Islands at Wachapreague Inlet, Cobb and Wreck Islands at Sand Shoal Inlet, and on the northwest side of Fisherman Island from September 1986 through September 1987. Although all life-stages were collected, the study was designed to focus on utilization of this area by juvenile finfish. Sixty-nine species of finfish were collected. Species diversity and abundance fluctuated widely among seasons. Both were highest in the fall and lowest in the winter. The most abundant species over all seasons and locations were silversides (*Menidia menidia*) and bay anchovy (*Anchoa mitchilli*). The most abundant commercially and recreationally important species collected were summer flounder (*Paralichthys dentatus*) and the sciaenids, croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*) and weakfish (*Cynoscion regalis*). As adults, these species migrate inward in the spring and leave in the fall, but newly recruited juveniles were found utilizing these areas almost all year. Comparisons were made with results from the only other directed study in this area (Richards and Castagna, 1970). Differences between the results of these two studies can be attributed to gear (size of trawl net mesh) and site (salinity and relative position in marsh).

Key words: fish, ecology, Virginia.

INTRODUCTION

Much of what is known about the fish fauna on the seaside of the Delmarva Peninsula is a compilation of ancillary data from species-specific studies (Hoese, 1962; Musick and Colvocoresses, 1987), site specific studies (Cowan and Birdsong, 1985; Kimmel, 1973), recreational and commercial fishing (Richards, 1965; Burrell *et al.*, 1972; Marshall and Lucy, 1981), or information gained from local watermen. Only one study, conducted for 12 months in 1965-66, has been directed at the ecology of finfish in this area. That survey covered a larger geographic area, Metompkin Bay to Fishermans Island, and a broader spectrum of habitats, inlets, channels, inshore beaches and tidal creeks (Richards and Castagna, 1970). The

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present study evaluated fewer sites, but in a more intensive manner with semi-monthly sampling of the same stations for 13 months.

The objective of this project was to describe the abundance, distribution, and seasonality of finfish species captured in waters behind the barrier islands of Virginia, with emphasis on utilization of these waters by juvenile fish, especially new recruits. It has been speculated that the seaside bays of the eastern shore of Virginia are primary nursery grounds for juvenile flatfish (Poole, 1966), however, this has never been documented with direct observations. Although the marsh areas of the Chesapeake Bay, Virginia (Weinstein and Brooks, 1983; Weinstein *et al.*, 1980; Smith *et al.*, 1984) and the open sand areas of Pamlico Sound, North Carolina (Powell and Schwartz, 1977), have been well studied and established as important nursery habitat for juvenile finfish, no analogous research has been conducted in the lagoonal areas behind the Virginia Barrier Islands. Therefore, the purpose of this study was to document the presence or absence of juvenile finfish over a 13-month period as a foundation for future research on the importance of this habitat.

METHODS

The eastern shore of Virginia forms the lower end of the Delmarva Peninsula, which is oriented in a north-south direction and separates the Atlantic Ocean from the Chesapeake Bay. The seaside of the peninsula is a contiguous system of shallow bays, extensive saltmarshes and barrier islands. The bays and saltmarshes are transected by main channels approximately 400-1000 m wide near inlets and 40-250 m wide at the upstream end (D. Wyanski, pers. comm.). Channel depths range from 3-20 m at Mean High Water (MHW).

Preliminary sampling at many eastern shore sites was conducted March through August 1986 (Norcross, 1987). Based on presence of juvenile finfish, accessibility, and diversity of habitat, three sites were selected for this study: Wachapreague [W] Channel and Inlet between Cedar and Parramore Islands; Sand Shoal [S] Channel and Inlet between Cobb and Wreck Islands; and Fishermans [F] Island (Figures 1-4). Since there is no background information on distribution of juvenile finfish in this area, a systematic survey was employed as appropriate for exploratory studies under such circumstances (Doubleday and Rivard, 1981). Therefore, the sites were chosen to cover a widespread geographic area which could be intensively sampled within a short period of time. Selected sites were similar with regard to proximity of barrier islands, extent of marshes, water depth, and creek size. Inherent differences in the morphology of the islands may affect the hydrography and, hence, the composition and distribution of fish.

At each site, sample stations were located in channels directly behind the barrier islands and adjacent to the marsh complex. Because of the lack of information regarding this area as a potential nursery for finfish, station positions were chosen to encompass a variety of depths, habitats and substrates. Sand substrate was found at inlets, creek mouths and along river margins. Mud substrate predominated in the creeks of the saltmarshes.

A bottom trawl is the preferred gear for collecting demersal fish (Hemmings, 1969) over unobstructed bottom. This study was conducted with a 4.9 m semi-balloon otter trawl with 19 mm bar mesh in the wings and upper body, 6.4 mm delta

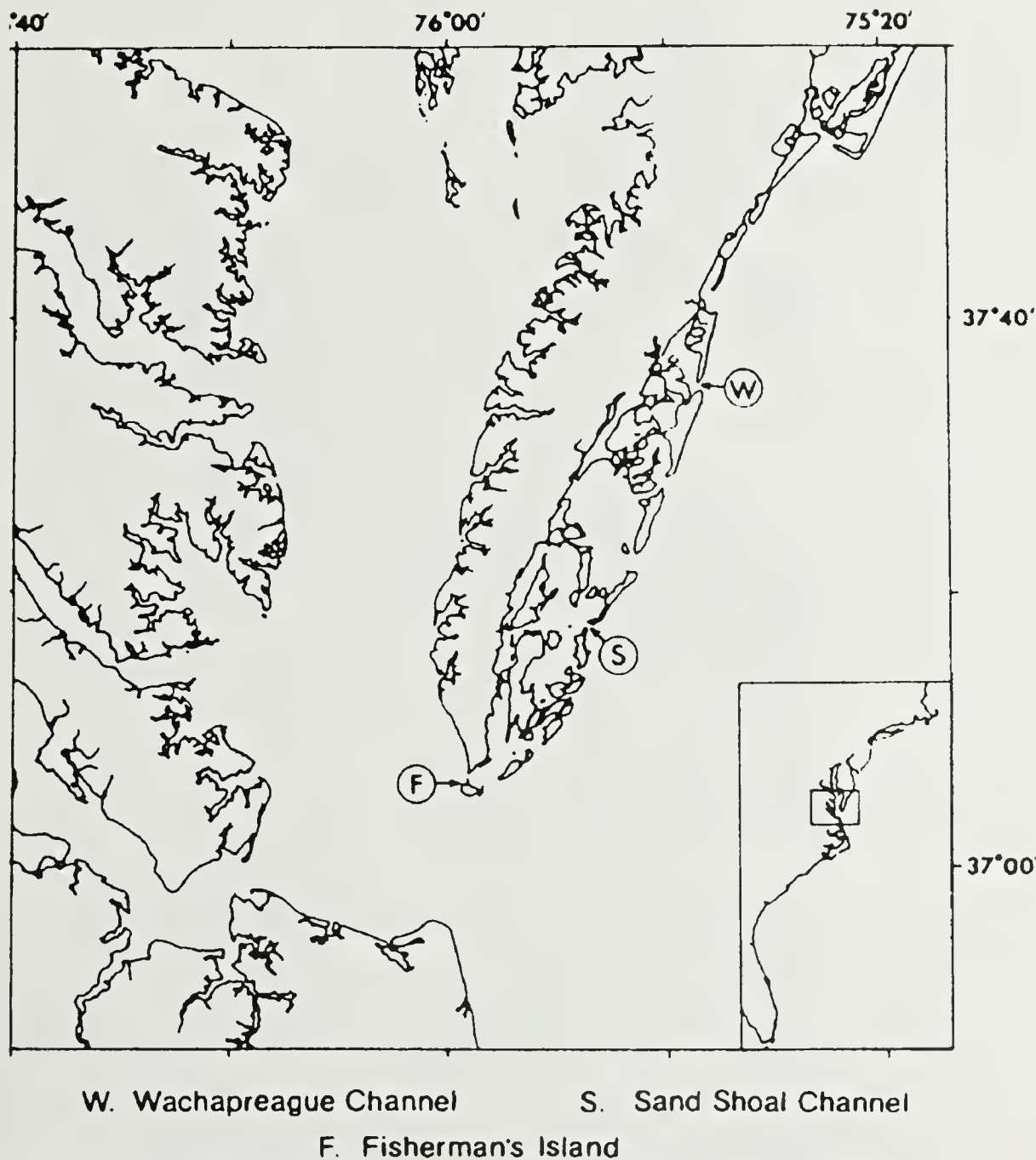


FIGURE 1. Location of sampling sites on the eastern shore of Virginia: Wachapreague, Sand Shoal and Fisherman Island.

mesh in the lower body and codend, and 3.2 mm delta mesh liner. This small mesh was chosen for this study specifically to capture newly recruited fish < 30 mm. The doors were 30.5 cm x 61 cm and weighed 6.4 kg each. A 4.8 mm link tickler chain was added, since the addition of a tickler chain to a trawl results in statistically significant increases in catches of demersal organisms (Chittenden and Van Engel, 1972; Creutzberg *et al.*, 1987). The trawl was deployed using 4.8 mm wire cable from an electric winch and a free-swinging davit aboard a 6.4 m open Privateer.

Two five-minute trawls were performed at each station, oriented with and against the current. Five-minute tows were chosen considering the mesh size of the liner, high biomass of the summer/fall fish catch, and shortness of winter days. Tow speed was 100-150 cm/sec over the bottom, following the convention of other



FIGURE 2. Location of sampling stations at Wachapreague Inlet: W1 - deep sand; W2 - shallow sand; W3 - mud seine; W4 - shallow mud; W5 - deep mud.

studies using the same size trawl (Orth and Heck, 1980; Weinstein and Brooks, 1983).

Seining is a commonly accepted method for assessing the abundance of juvenile fish (Lyons, 1986). Two seine hauls, 25 m in length, were made parallel to the shore at each site, one with the current and one against the current. A 6.1 m bag seine (3.2 mm delta mesh) was modified by the addition of a 3.2 mm link chain to the leadline which acted as a tickler chain. This enabled the seine to disturb the top 1 cm of substrate, enhancing the capture of very small (<25 mm) flatfish.

The sampling protocol for each site included four trawl stations, at deep (8.5-11.3 m) and shallow (1.2-1.8 m) sand substrates and deep (6.4-9.8 m) and shallow (1.2-1.8 m) mud substrates, and one seine station in <1 m of water on mud substrate. Specific locations of sample stations are shown in Figures 2 - 4. Seining was the only sampling method employed at Fisherman Island because of limited water depth. Tide stage controlled when certain locations could be sampled. All seine stations had to be sampled at or near low tide. Mud stations were sampled near low tide, and sand stations were sampled near high tide. Samples were collected twice monthly from September 1986 through mid-September 1987, for a total of 25 collections at each site. The frequency of the sampling was designed to capture newly recruiting juveniles. All fish were identified, enumerated, and discarded. Total length was measured for all flatfish and all sciaenids. Air, surface,

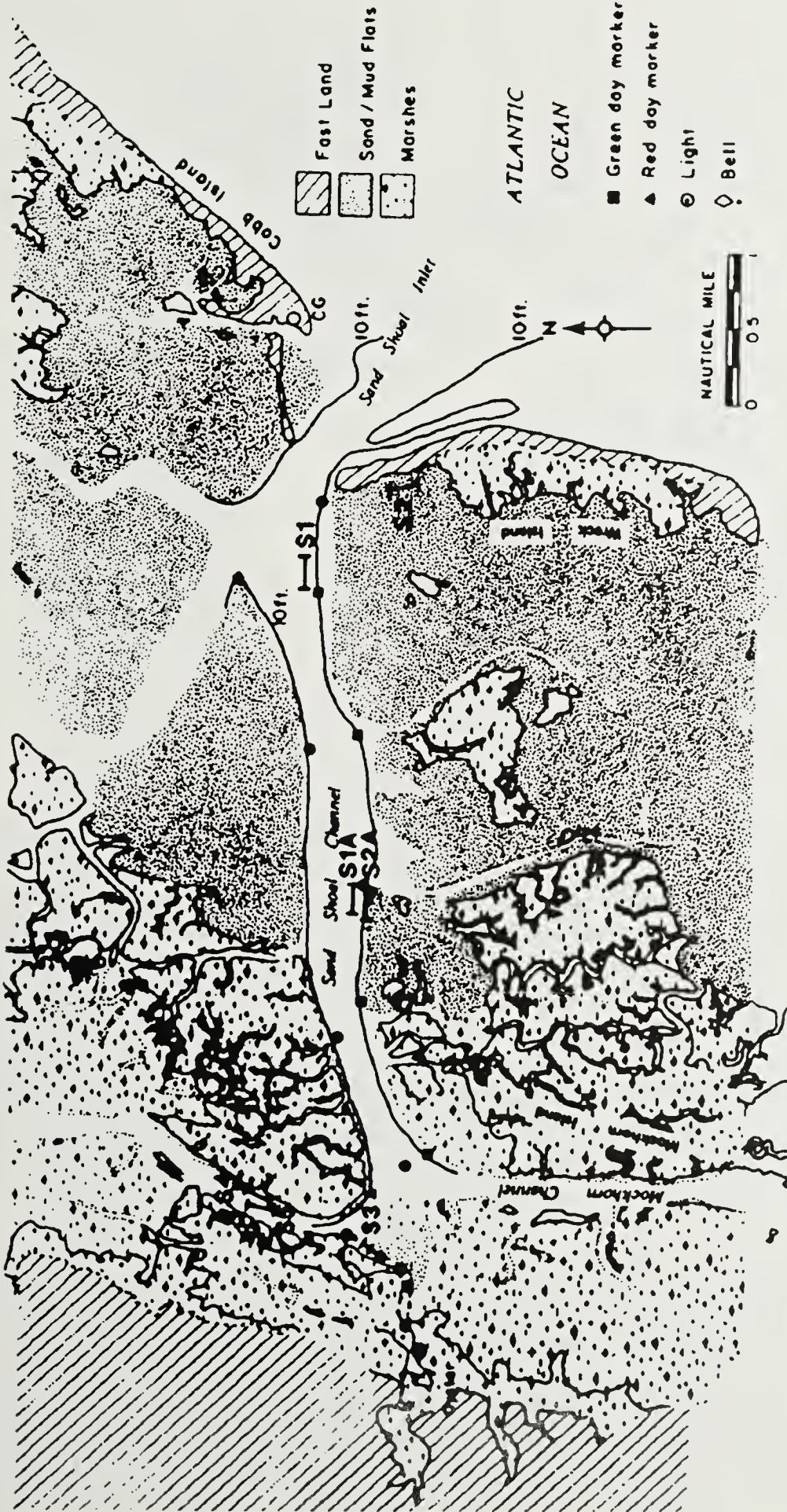


FIGURE 3. Location of sampling stations at Sand Shoal Inlet: S1 - deep sand; S1A n - alternate S1; S2 - shallow sand; S2A - alternate; S3 - mud seine; S4 - shallow mud; S5 - deep mud.

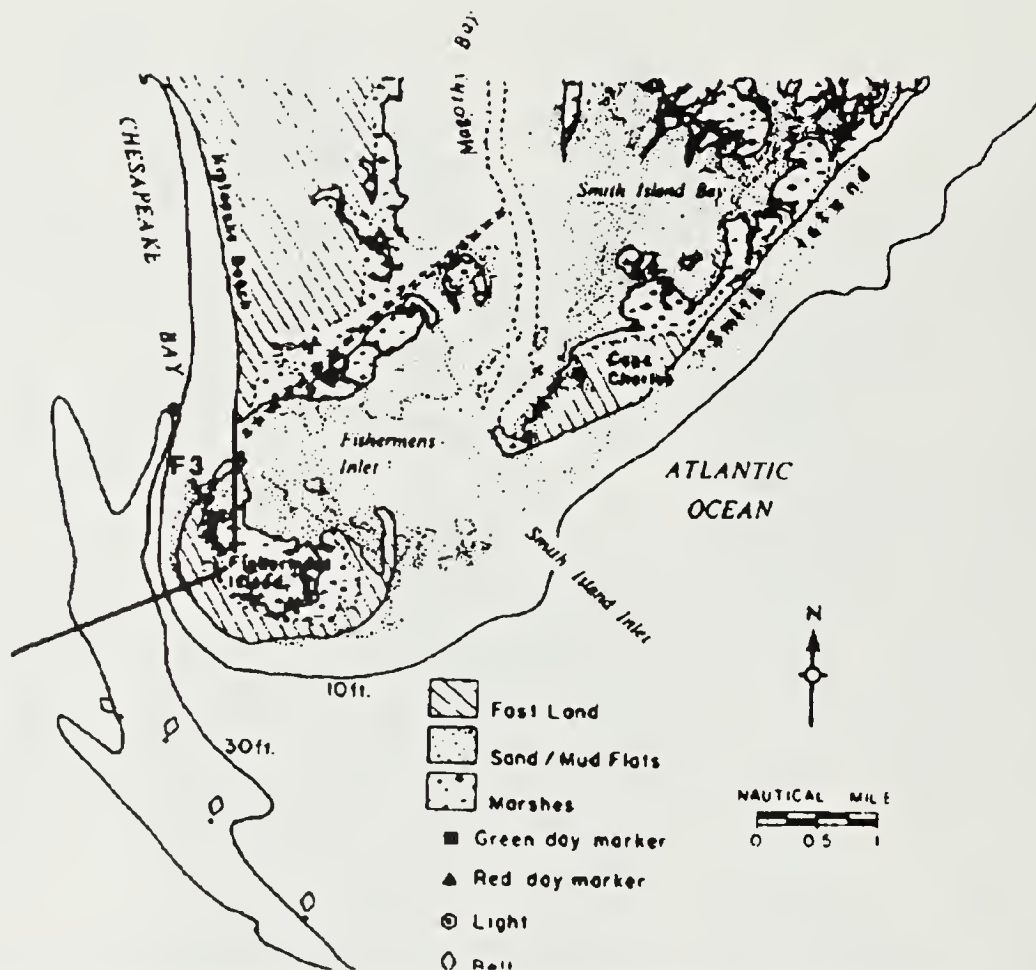


FIGURE 4. Location of sampling station at Fisherman Island: F3 - mud seine only.

and bottom water temperatures and surface and bottom salinities were recorded at each station.

The protocol employed by Richards and Castagna (1970) sampled 20 stations for a total of 376 samples between 22 June 1965 and 7 July 1966. No sampling was conducted in January. Eight trawl stations were sampled monthly October through March, and at two- to three-week intervals the remainder of the year. The depth of the trawl stations ranged from 1.8 to 12.2 (average 7.4 m). Tows were double the time (ten minutes) using a 4.9 m trawl with much larger mesh (32 mm bag, 13 mm liner) than that used in the present study. No seining was conducted October through April. Twelve seine stations with depth ranges of 1.0 - 1.7 m (average - 1.4 m) were occupied at two- to three-week intervals the remainder of the year. The mesh size (6.4 mm) of their seine was twice that used in the present study.

RESULTS

A total of 80 taxa of finfish were collected at all three sites, with 69 identified to species. When species identification was uncertain, fish were identified to the lowest taxonomic level possible, therefore, eight were classified to genus and three to order. Compared with Richards and Castagna (1970), our total missed 15 species, but included 15 additional species not captured by them. There was an overlap of 54 species. The top 28 most abundant species also were captured in the previous study. Comparison of our results with those of Richards and Castagna

TABLE 1. Fish species collected from the barrier island lagoons of the seaside of Virginia's eastern shore (nomenclature after Robins *et al.*, 1980).

| Species collected Taxonomic Group | | This Study | Richards & Castagna (1970) |
|--------------------------------------|---------------------------------------|---------------|----------------------------------|
| TRIAKIDAE | Smoothhound sharks | | |
| <i>Mustelus canis</i> | smooth dogfish | 30 | 18 |
| RAJIIDAE | Skates | | |
| <i>Raja eglanteria</i> | clearnose skate | 43 | 28 |
| DASYATIDAE | Stingrays | | |
| <i>Dasyatid</i> sp. | | 1 | 0 |
| <i>Dasyatis sayi</i> | bluntnose stingray | 13 | 1 |
| <i>Dasyatis americana</i> | southern stingray | 0 | 1 |
| <i>Dasyatis centroura</i> | rougtail stingray | 0 | 5 |
| <i>Gymnura micrura</i> | smooth butterfly ray | 0 | 4 |
| MYLIOBATIDAE | Eagle rays | | |
| <i>Myliobatis fremenvillei</i> | bullnose ray | 1 | 0 |
| ELOPIDAE | Tarpons | | |
| <i>Elops saurus</i> | ladyfish | 1 | 1 |
| ANGUILLIFORMES | | | |
| <i>Leptocephalus</i> larvae | unidentified | 10 | 0 |
| Glass eel | unidentified | 14 | 0 |
| ANGUILLIDAE | Freshwater eels | | |
| | <i>Anguilla rostrata</i> American eel | | 21 |
| CONGRIDAE | Conger eels | | |
| <i>Conger oceanicus</i> | conger eel | 16 | 2 |
| CLUPEIDAE | Herrings | | |
| <i>Alosa aestivalis</i> | blueback herring | 3 | 41 |
| <i>Alosa pseudoharengus</i> | alewife | 5 | 2 |
| <i>Alosa sapidissima</i> | American shad | 2 | 1 |
| <i>Brevoortia tyrannus</i> | Atlantic menhaden | 18 | 1057 |
| <i>Clupea harengus</i> | Atlantic herring | 0 | 11 |
| ENGRAULIDAE | Anchovies | | |
| <i>Anchoa hepsetus</i> | striped anchovy | 6 | 175 |
| <i>Anchoa mitchilli</i> | bay anchovy | 3214 | 3840 |
| SYNODONTIDAE | Lizardfishes | | |
| <i>Synodus foetens</i> | inshore lizardfish | 8 | 6 |

| | | | |
|----------------------------------|------------------------|---------|-------|
| BATRACHOIDIDAE | Toadfishes | | |
| <i>Opsanus tau</i> | oyster toadfish | 53 | 50 |
| GADIDAE | Codfishes | | |
| <i>Urophysis chuss</i> | red hake | 41 | 9 |
| <i>Urophysis regia</i> | spotted hake | 337 | 20 |
| <i>Urophysis tenuis</i> | white hake | 4 | 0 |
| | Pollachius virens | pollock | 0 |
| OPHIDIIDAE | Cusk-eels | | |
| <i>Ophidiid</i> sp. | | 2 | 0 |
| <i>Lepophidium cervinum</i> | fawn cusk-eel | 34 | 0 |
| <i>Ophidion marginatum</i> | striped cusk-eel | 62 | 2 |
| EXOCOETIDAE | Flying fishes | | |
| <i>Hyporhamphus unifasciatus</i> | halfbeak | 0 | 4 |
| BELONIDAE | Needlefishes | | |
| <i>Belonid</i> sp. | | 1 | 0 |
| <i>Strongylura marina</i> | Atlantic needlefish | 6 | 0 |
| CYPRINODONTIDAE | Killifishes | | |
| <i>Cyprinodon variegatus</i> | sheepshead minnow | 24 | 4893 |
| <i>Lucania parva</i> | rainwater killifish | 408 | 31 |
| <i>Fundulus heteroclitus</i> | mummichog | 1209 | 13800 |
| <i>Fundulus majalis</i> | striped killifish | 84 | 8590 |
| <i>Fundulus luciae</i> | spotfin killifish | 0 | 25 |
| ATHERINIDAE | Silversides | | |
| <i>Menidia beryllina</i> | inland silverside | 11042 | 30424 |
| <i>Menidia menidia</i> | Atlantic silverside | 1 | 11 |
| <i>Membras martinica</i> | rough silverside | 0 | 28 |
| GASTEROSTEIDAE | Sticklebacks | | |
| <i>Gasterosteus aculeatus</i> | threespine stickleback | 5 | 1 |
| <i>Apeltes quadracus</i> | fourspine stickleback | 0 | 3 |
| SYNGNATHIDAE | Pipefishes | | |
| <i>Hippocampus erectus</i> | lined seahorse | 28 | 3 |
| <i>Syngnathus fuscus</i> | northern pipefish | 107 | 36 |
| <i>Syngnathus floridae</i> | dusky pipefish | 5 | 0 |
| PERCICHTHYIDAE | Temperate basses | | |
| <i>Centropristis striata</i> | black seabass | 125 | 105 |
| POMATOMIDAE | Bluefishes | | |
| <i>Pomatomus saltatrix</i> | bluefish | 5 | 5 |

| | | | |
|---------------------------------|-----------------------|------|------|
| CARANGIDAE | Jacks | | |
| <i>Selene vomer</i> | lookdown | 2 | 0 |
| <i>Caranx hippos</i> | crevalle jack | 0 | 2 |
| <i>Trachinotus falcatus</i> | permit | 0 | 2 |
| LUTJANIDAE | Snappers | | |
| <i>Lutjanus griseus</i> | gray snapper | 4 | 0 |
| GERREIDAE | Mojarras | | |
| <i>Gerreid</i> sp. | | 6 | 0 |
| <i>Eucinostomus argenteus</i> | spotfin mojarra | 5 | 0 |
| HAEMULIDAE | Grunts | | |
| <i>Orthopristis chrysoptera</i> | pigfish | 18 | 59 |
| SPARIDAE | Porgies | | |
| <i>Stenotomus chrysops</i> | scup | 3 | 49 |
| SCIAENIDAE | Drums | | |
| <i>Bairdiella chrysoura</i> | silver perch | 307 | 1077 |
| <i>Leiostomus xanthurus</i> | spot | 1551 | 28 |
| <i>Micropogonias undulatus</i> | Atlantic croaker | 2021 | 9 |
| <i>Pogonias chromis</i> | black drum | 1 | 23 |
| <i>Cynoscion regalis</i> | weakfish | 399 | 39 |
| <i>Cynoscion nebulosus</i> | spotted seatrout | 3 | 0 |
| <i>Sciaenops ocellata</i> | red drum | 5 | 0 |
| <i>Menticirrhus</i> sp. | | 3 | 0 |
| <i>Menticirrhus saxatilis</i> | northern kingfish | 47 | 97 |
| <i>Menticirrhus americanus</i> | southern kingfish | 7 | 0 |
| MULLIDAE | Goatfishes | | |
| <i>Mullus auratus</i> | red goatfish | 0 | 1 |
| CHAETODONTIDAE | Butterflyfishes | | |
| <i>Chaetodon ocellatus</i> | spotfin butterflyfish | 3 | 0 |
| LABRIDAE | Wrasses | | |
| <i>Tautoga onitis</i> | tautog | 5 | 21 |
| MUGILIDAE | Mulletts | | |
| <i>Mugil cephalus</i> | striped mullet | 44 | 423 |
| <i>Mugil curema</i> | white mullet | 0 | 504 |
| SPHYRAENIDAE | Barracudas | | |
| <i>Sphyraena borealis</i> | northern sennet | 0 | 4 |
| URANOSCOPIDAE | Stargazers | | |
| <i>Astroscopus guttatus</i> | northern stargazer | 6 | 1 |
| BLENNIIDAE | Combtooth blennies | | |
| <i>Hypsoblennius hentzi</i> | feather blenny | 19 | 0 |
| <i>Chasmodes bosquianus</i> | striped blenny | 7 | 0 |

| | | | |
|--------------------------------------|-----------------------|-----|-----|
| GOBIIDAE | Gobies | | |
| <i>Gobionellus</i> sp. | | 11 | 0 |
| <i>Gobionellus boleosoma</i> | darter goby | 13 | 0 |
| <i>Gobiosoma</i> sp. | | 1 | 0 |
| <i>Gobiosoma ginsburgi</i> | seaboard goby | 136 | 1 |
| <i>Gobiosoma bosci</i> | naked goby | 104 | 48 |
| <i>Microgobius thalassinus</i> | green goby | 5 | 1 |
| STROMATEIDAE | Butterfishes | | |
| <i>Peprilus triacanthus</i> | butterfish | 18 | 12 |
| <i>Peprilus alepidotus</i> | harvestfish | 2 | 0 |
| TRIGLIDAE | Searobins | | |
| <i>Prionotus carolinus</i> | northern searobin | 109 | 72 |
| <i>Prionotus evolans</i> | striped searobin | 10 | 11 |
| PLEURONECTIFORMES | | | |
| flatfish | unidentified | 1 | 0 |
| BOTHIDAE | Lefteye flounders | | |
| <i>Etropus</i> sp. | | 1 | 0 |
| <i>Etropus crossotus</i> | fringed flounder | 34 | 6 |
| <i>Etropus microstomus</i> | smallmouth flounder | 351 | 61 |
| <i>Paralichthys dentatus</i> | summer flounder | 927 | 66 |
| <i>Scophthalmus aquosus</i> | windowpane | 129 | 21 |
| PLEURONECTIDAE | Righteye flounders | | |
| <i>Pseudopleuronectes americanus</i> | winter flounder | 51 | 203 |
| SOLEIDAE | Soles | | |
| <i>Trinectes maculatus</i> | hogchoker | 447 | 2 |
| CYNOGLOSSIDAE | Tonguefishes | | |
| <i>Symphurus plagiusa</i> | blackcheek tonguefish | 833 | 11 |
| BALISTIDAE | leatherjackets | | |
| <i>Monocanthus hispidus</i> | planehead filefish | 0 | 2 |
| TETRAODONTIDAE | Puffers | | |
| <i>Sphoeroides maculatus</i> | northern puffer | 30 | 117 |
| DIODONTIDAE | Porcupinefishes | | |
| <i>Chilomycterus schoepfi</i> | striped burrfish | 11 | 5 |

(1970) shows large numerical differences, sometimes one to two orders of magnitude, of individual species caught (Table 1). Flatfish and sciaenids comprised 12.8% and 20.3% of our total catch.

Temperature and salinity were averaged over all stations at the two primary sites for the semi-monthly sampling period. They fluctuated seasonally as expected (Fig.

5). There was usually little difference between surface and bottom samples. The variation between Wachapreague and Sand Shoal was usually slight, though Wachapreague was generally a few degrees cooler in the spring and summer. Seasonal variations in salinities were greater at Wachapreague than at Sand Shoal. The station at Fisherman Island was within the marsh complex and further away from a main channel than the other sites, and therefore had markedly lower salinities.

The number of species collected by all gear at all stations shows strong seasonal variation with diversity lowest in the winter and highest in the fall (Fig. 6). There were approximately the same number of species at any time at Wachapreague and Sand Shoal which had equal sampling effort. At Fisherman Island, where there was a reduced sampling effort, fewer species were collected. The combined number of species is greater than at the individual sites, suggesting between-site differences in species composition. A seasonal cycle in abundance was seen in flatfish and sciaenids, with winter having the fewest individuals. The catch-per-unit-effort (trawl or seine) of sciaenids is an order of magnitude greater than that of flatfish in the spring and fall, but drops off to zero in the late winter (Fig. 7). The pronounced decrease in catch seen for all species in February may be an artifact of sampling error due to weather or effectiveness of gear. This seasonal pattern of relative diversity and abundance is evident when data are grouped into three-month seasons: Fall = October, November, December; Winter = January, February, March; Spring = April, May, June; Summer = July, August, September (Table 2).

Atlantic silversides (*Menidia menidia*) and bay anchovy (*Anchoa mitchilli*) were ranked among the top three across all seasons. Mummichog (*Fundulus heteroclitus*) and summer flounder (*Paralichthys dentatus*) also were ranked among the top 12 during all seasons. Eleven species, blackcheek tonguefish (*Symphurus plagiusa*), rainwater killifish (*Lucania parva*), smallmouth flounder (*Etropus microstomus*), seaboard goby (*Gobiosoma ginsburgi*), windowpane flounder (*Scophthalmus aquosus*), black seabass (*Centropristis striata*), northern pipefish (*Syngnathus fuscus*), naked goby (*Gobiosoma bosci*), striped killifish (*Fundulus majalis*), striped cusk eel (*Ophidion marginatum*), and oyster toad fish (*Opsanus tau*), were collected during all seasons resulting in a year-round fauna of 15 species. Additionally, spot (*Leiostomus xanthurus*), hogchoker (*Trinectes maculatus*), and spotted hake (*Urophycis regis*), were captured and ranked in three of four seasons. However, only nine of those species were classified among the 11 resident species described by Richards and Castagna (1970). Richards and Castagna (1970) also included sheepshead minnow (*Cyprinodon variegatus*) and spotfin killifish (*Fundulus luciae*) which were not collected in this study.

The abundance of many of the top-ranking species fluctuates according to season, with several being important during only one three-month period. This is a result of season-specific influxes of new recruits, as demonstrated by the single-season high rank of croaker (*Micropogonias undulatus*), weakfish (*Cynoscion regalis*), and silver perch (*Bairdiella chrysoura*). Four other species, northern searobin (*Prionotus carolinus*), striped mullet (*Mugil cephalus*), red hake (*Urophycis chuss*), and American eel (*Anguilla rostrata*), ranked low in one season and were unranked, though present, in two other seasons.

TABLE 2. Top 12 most abundant species per season. Number is rank, dot indicates presence without rank in top 12, blank means species not captured that season. Overall is rank yearly abundance.

| SPECIES | Overall | Fall | Winter | Spring | Summer |
|-----------------------|---------|------|--------|--------|--------|
| Atlantic silverside | 1 | 2 | 1 | 2 | 1 |
| Bay anchovy | 2 | 3 | 2 | 1 | 2 |
| Atlantic croaker | 3 | 1 | . | | . |
| Spot | 4 | 7 | | 3 | 3 |
| Mummichog | 5 | 5 | 10 | 6 | 4 |
| Summer flounder | 6 | 8 | 4 | 4 | 6 |
| Blackcheek tonguefish | 7 | 6 | . | 5 | 9 |
| Hogchoker | 8 | 8 | | 9 | 7 |
| Rainwater killifish | 9 | 4 | . | . | 9 |
| Weakfish | 10 | . | | . | 5 |
| Smallmouth flounder | 11 | 10 | 8 | 8 | . |
| Spotted hake | 12 | 11 | 3 | 7 | |
| Silver perch | 13 | 12 | | . | 8 |
| Seaboard goby | 14 | . | 7 | . | . |
| Windowpane | 15 | . | 6 | . | . |
| Black seabass | 16 | . | . | 11 | . |
| Northern searobin | 17 | . | | 10 | . |
| Northern pipefish | 18 | . | . | 12 | . |
| Naked goby | 19 | . | . | . | 11 |
| Striped killifish | 20 | . | 5 | . | . |
| Striped cuskeel | 21 | . | . | . | . |
| Oyster toadfish | 22 | . | . | . | 12 |
| Striped mullet | 25 | | 11 | . | |
| Red hake | 27 | . | 9 | . | |
| American eel | 34 | . | 12 | | . |

DISCUSSION

The top two ranks were always held by Atlantic silversides or bay anchovies, except when usurped by the fall influx of croaker. Abundance of silversides is an order of magnitude higher than anchovies (Fig. 8). A site-specific difference is apparent, with the abundance of both species peaking at Sand Shoal one month before peaking at Wachapreague. Abundance was consistently lower at Fisherman Island, even for Atlantic silversides which had higher catch rates in seines than trawls. The higher abundance at Wachapreague may be due to physical parameters and habitat preferences; there is more open water at Sand Shoal and more marsh area at Wachapreague. Though abundant year-round, both of these species display a seasonal pattern, with peak abundances in the spring and summer caused by newly-spawned recruits. These seasonal patterns hold for both trawl and seine catches. Although neither species leaves the area in the winter, abundance decreases. These decreases in fish abundance may be attributed to mortality, local movement to unsampled areas, or seasonal differential in availability to sampling gear.

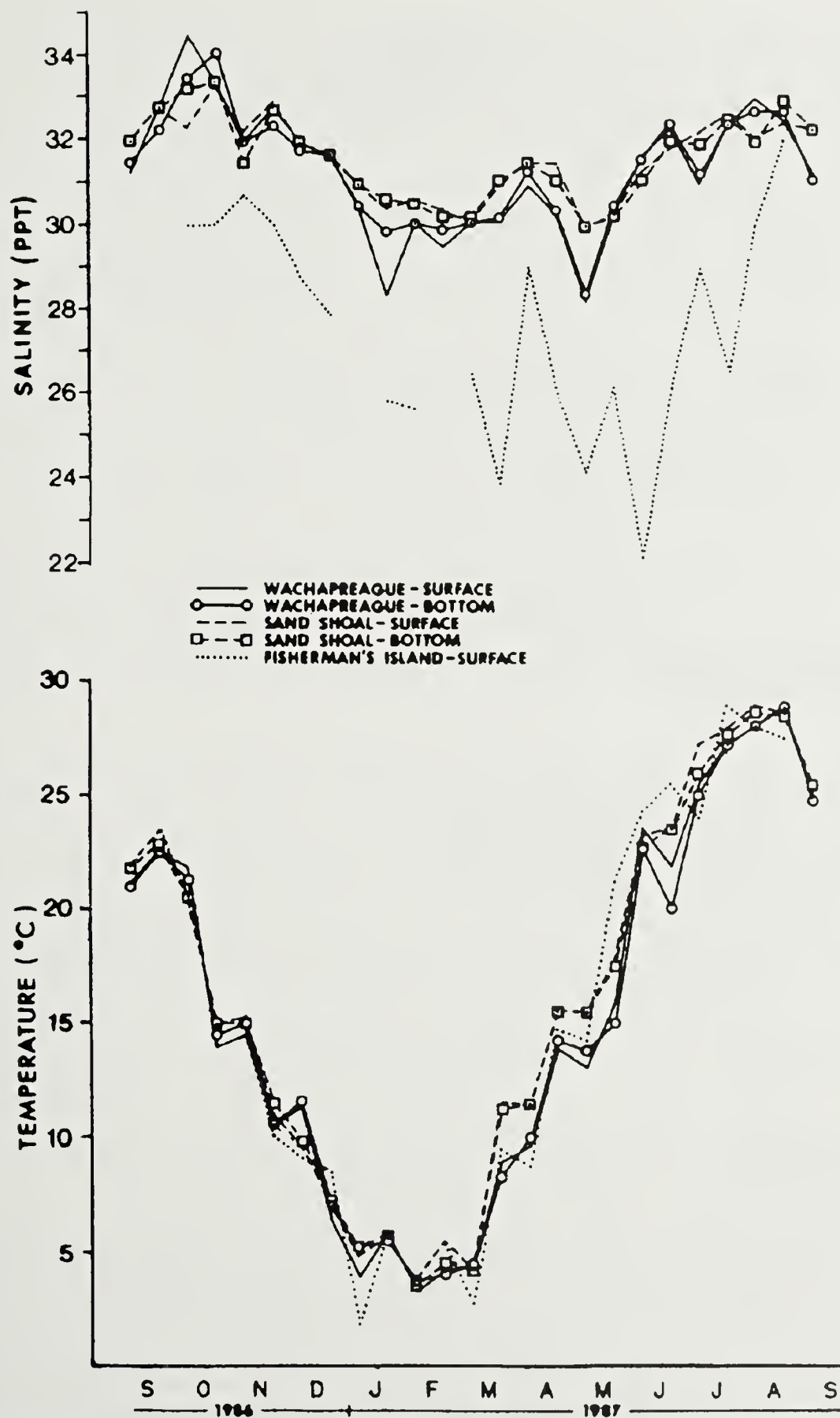


FIGURE 5. Semi-monthly surface and bottom salinity and temperature averaged over all stations at each site, September 1986 - September 1987.

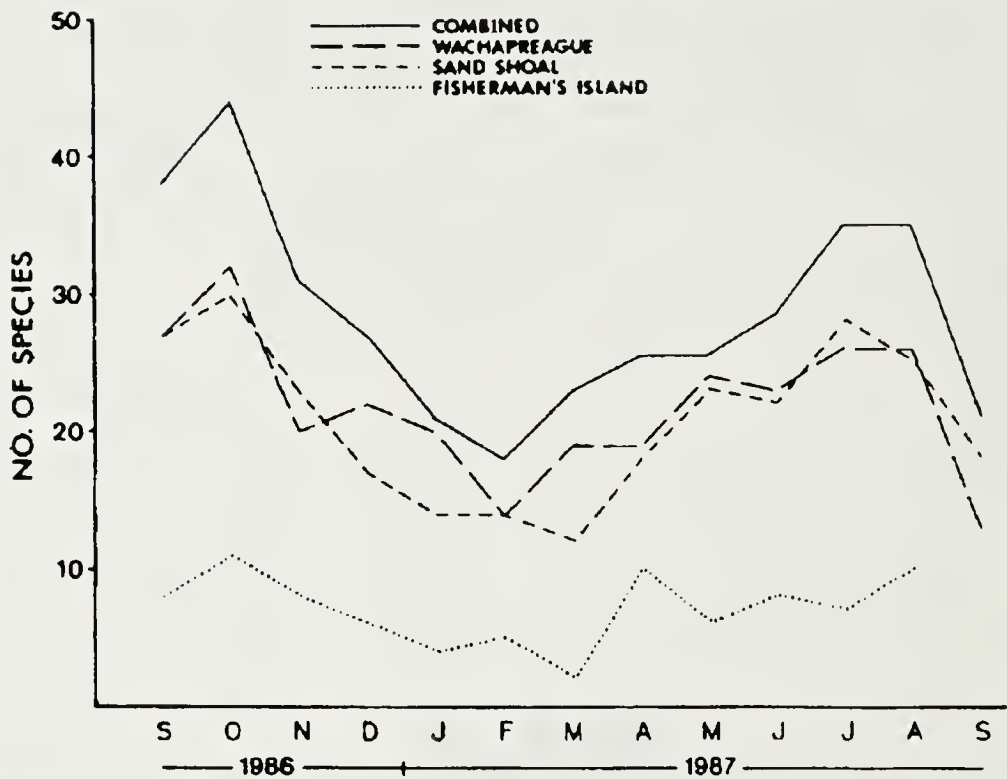


FIGURE 6. Number of fish species collected at each site and sites combined each month, September 1986 - September 1987.

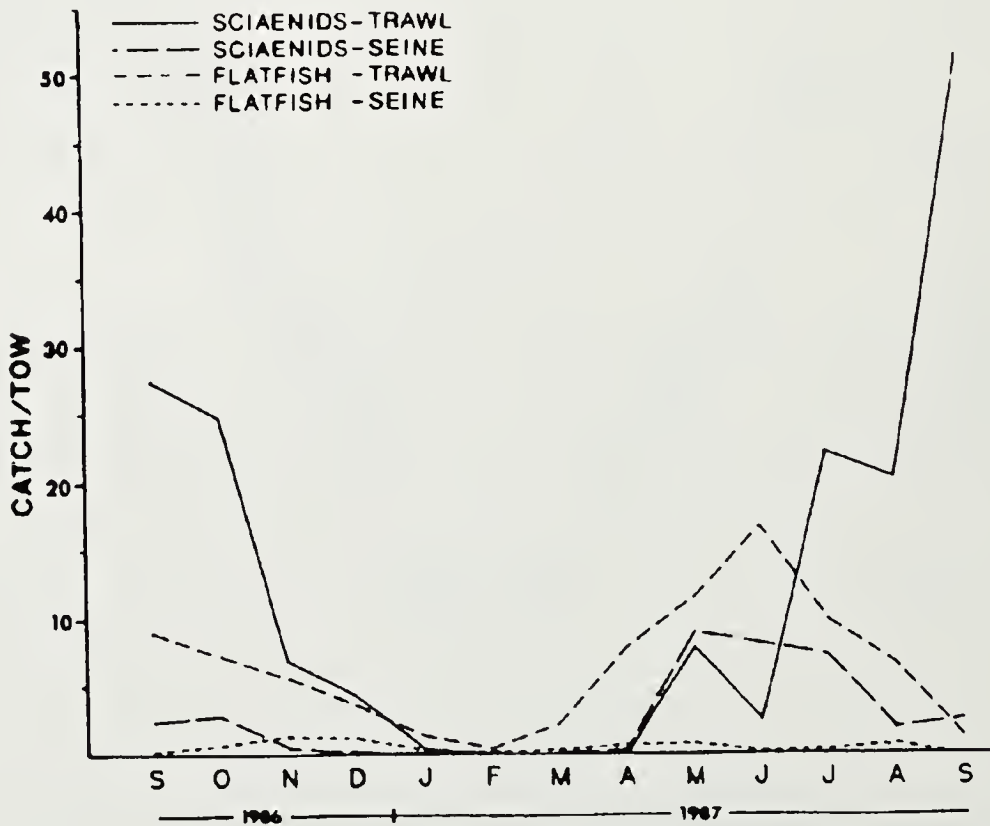


FIGURE 7. Catch/tow (5 min trawl or 25 m seine) of sciaenids and flatfishes by gear, sites combined, September 1986 - September 1987.

Mummichog, rainwater killifish, and spotted hake (Fig. 9) are the only other non-flatfish and non-sciænid species among the overall top 12. Again, a seasonal pattern is observed, with decreased numbers in January, February and March for the two summer-spawning marsh killifish. Rainwater killifish are only found at Fisherman Island. Although fairly abundant at Sand Shoal in the fall, mummichogs are most abundant at Fisherman Island in the spring and summer. In contrast, spotted hake exhibited a reverse pattern, with no individuals captured in the summer months. Spotted hake spawn offshore of the Chesapeake Bay from September through March (Hardy, 1978), coincident with the pattern of abundance noted in this study (Fig. 9).

After small marsh fishes, sciænids are the next most abundant group. As a group they exhibit a pattern similar to that of the other species, *i. e.*, low abundance in the winter and high in the spring, summer and fall. However, individually this pattern is not seen (Fig. 10). Seasonal occurrence of recruits reflects the spawning seasons of the four sciænids, croaker - fall, spot - winter, weakfish and silver perch - summer (Johnson, 1978). Most of the sciænids captured in this study were newly recruited juveniles. At time of first appearance, croaker were as small as 6 mm, silver perch - 12 mm, weakfish - 14 mm, and spot - 17 mm. Seasonal patterns do not appear consistent between years, as the abundance of all sciænids differs greatly between September 1986 and September 1987. Spot is the only sciænid that occurs in abundance in seine catches and was therefore collected at Fisherman Island.

Flatfish consistently occur in the barrier island lagoons, but at levels of abundance one to two orders of magnitude smaller than silversides, anchovies and sciænids. They are rarely captured at Fisherman Island, perhaps because they are less susceptible to capture by seine. Seasonal fluctuation of flatfish abundance on the seaside of the eastern shore is quite pronounced (Fig. 11) as the flatfishes migrate out of the study area in the winter. Summer flounder are the only flatfish present all year with winter and spring abundance consisting mainly of recently recruited individuals. A spring influx can be seen beginning in March or April for all species with winter flounder as small as 10 mm, summer flounder - 13 mm, smallmouth flounder and blackcheek tonguefish - 17 mm, and windowpane flounder - 29 mm. Summer flounder of all sizes are consistently more abundant at Wachapreague, the "flounder capital of the world."

Richards and Castagna (1970) collected consistently larger numbers of killifishes (Cyprinodontidae), silversides (Atherinidae), and mullets (Mugilidae) than this study and we consistently captured larger numbers of flatfish (Bothidae, Soleidae, Cynoglossidae), drums (Sciænidae), hake (Gadidae), cusk-eels (Ophidiidae), pipefishes (Syngnathidae), and gobies (Gobiidae) than captured in their study. Both studies used the same size trawl, but these differences in abundance can be partially attributed to the small-mesh net (6.4 mm versus 32 mm) and liner (3.2 mm versus 13 mm) we used which captured smaller newly recruited fish than the earlier study. Another factor contributing to the difference was station location. Our only site not adjacent to a main channel was Fisherman Island. The lower salinity and fish abundance at that site demonstrates the bias introduced by site selection. Richards and Castagna (1970) had several stations within tidal

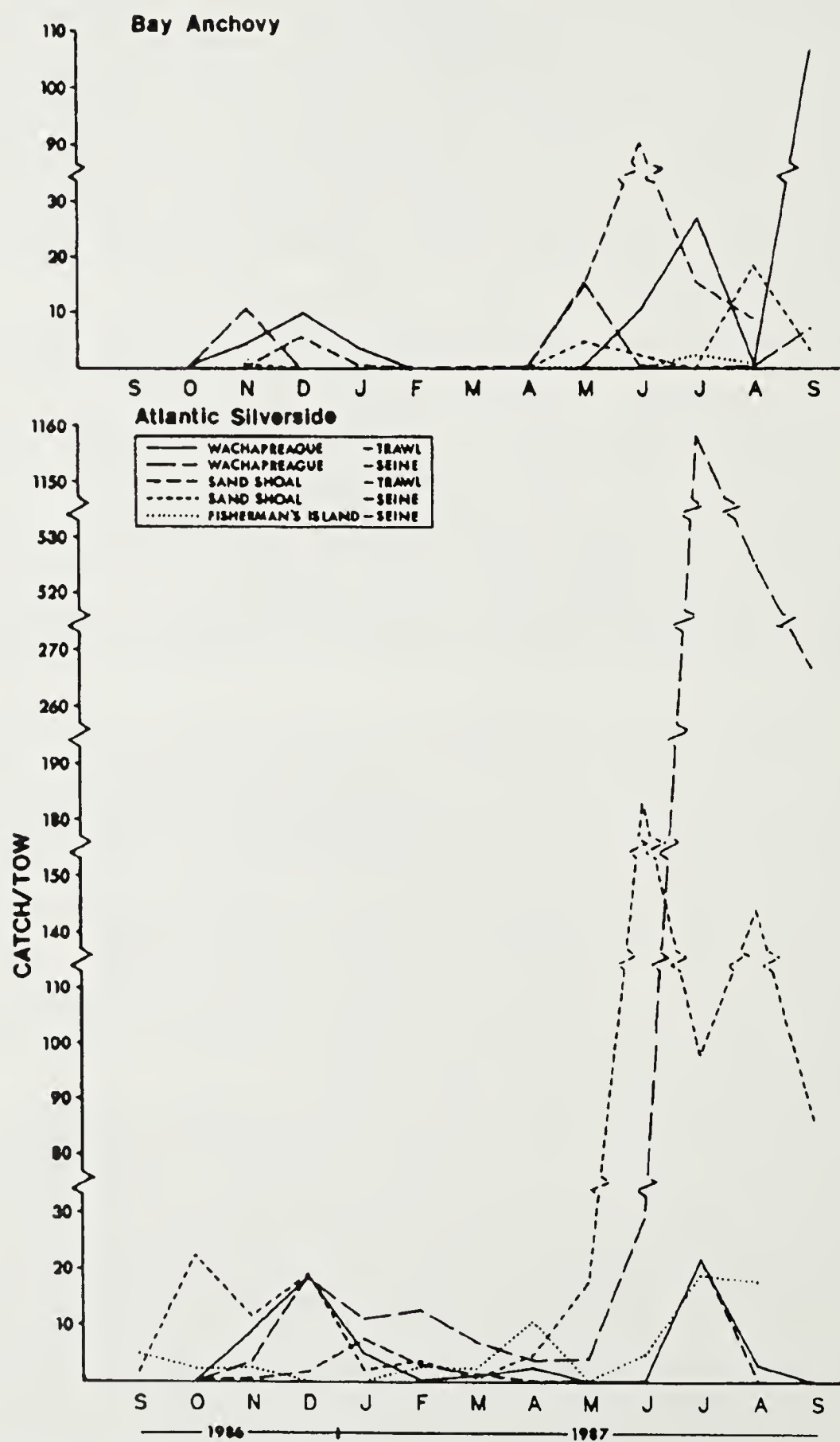


FIGURE 8. Catch/tow (5 min trawl or 25 m seine) of Atlantic silverside and bay anchovy by site, September 1986 - September 1987.

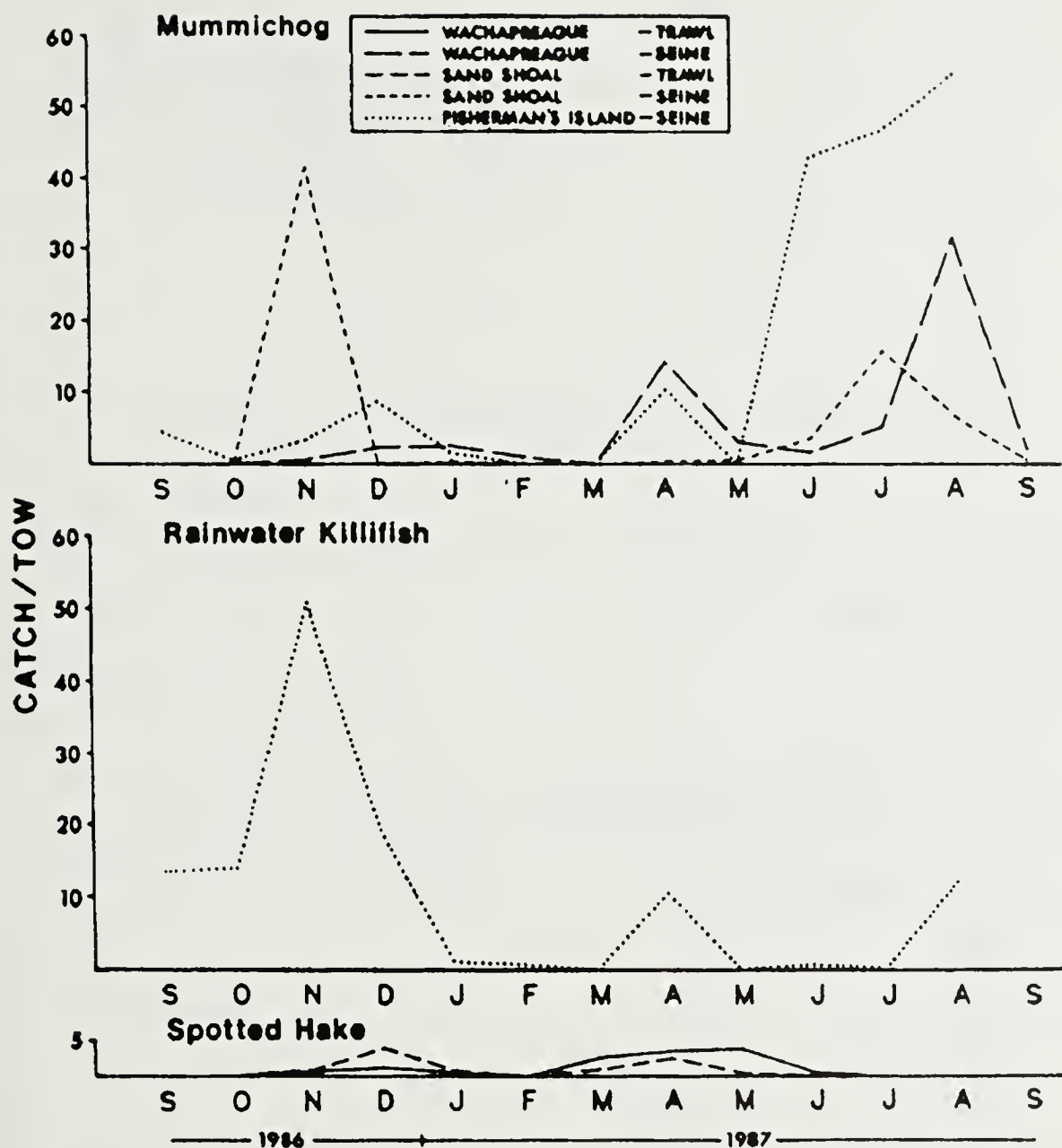


FIGURE 9. Catch/tow (5 min trawl or 25 m seine) of mummichog, rainwater killifish and spotted hake by site, September 1986 - September 1980.

creeks which we did not, thus accounting for their capture of more high marsh, lower salinity species.

CONCLUSIONS

The lagoonal areas behind the Virginia Barrier Islands have a dynamic fish population. This study provides an assessment of seasonality, distribution, and abundance of finfish in these waters. It is the first documentation of juvenile finfish use of these waters and demonstrates the presence of at least one juvenile sciaenid or flatfish during every season. The differences between the results of this study and that of Richards and Castagna (1970) can be attributed to size selectivity of the gear, inclusion of juvenile lifestages, and sampling locations. Because of the

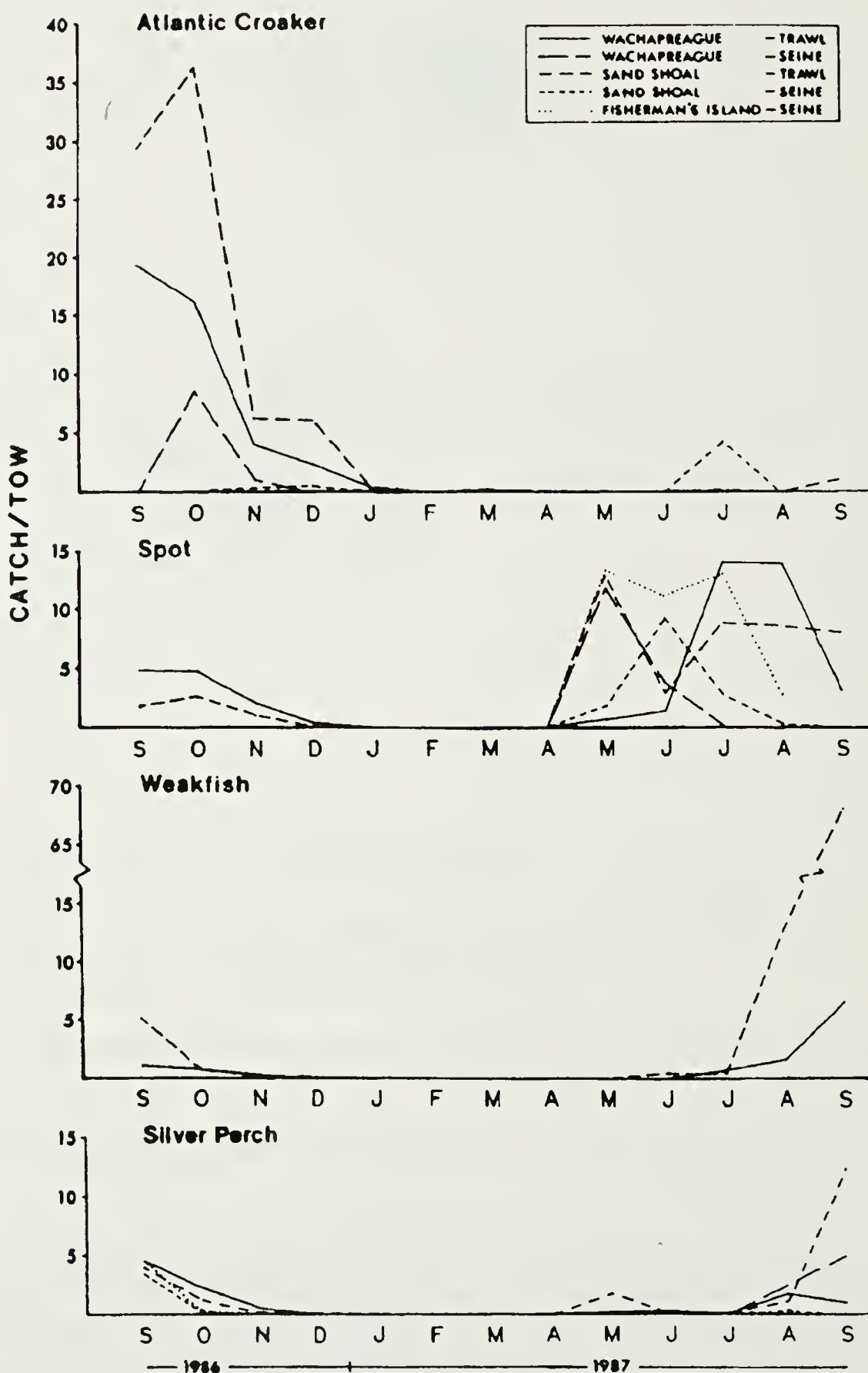


FIGURE 10. Catch/tow (5 min trawl or 25 m seine) of dominant sciaenids by site, September 1986 - September 1987.

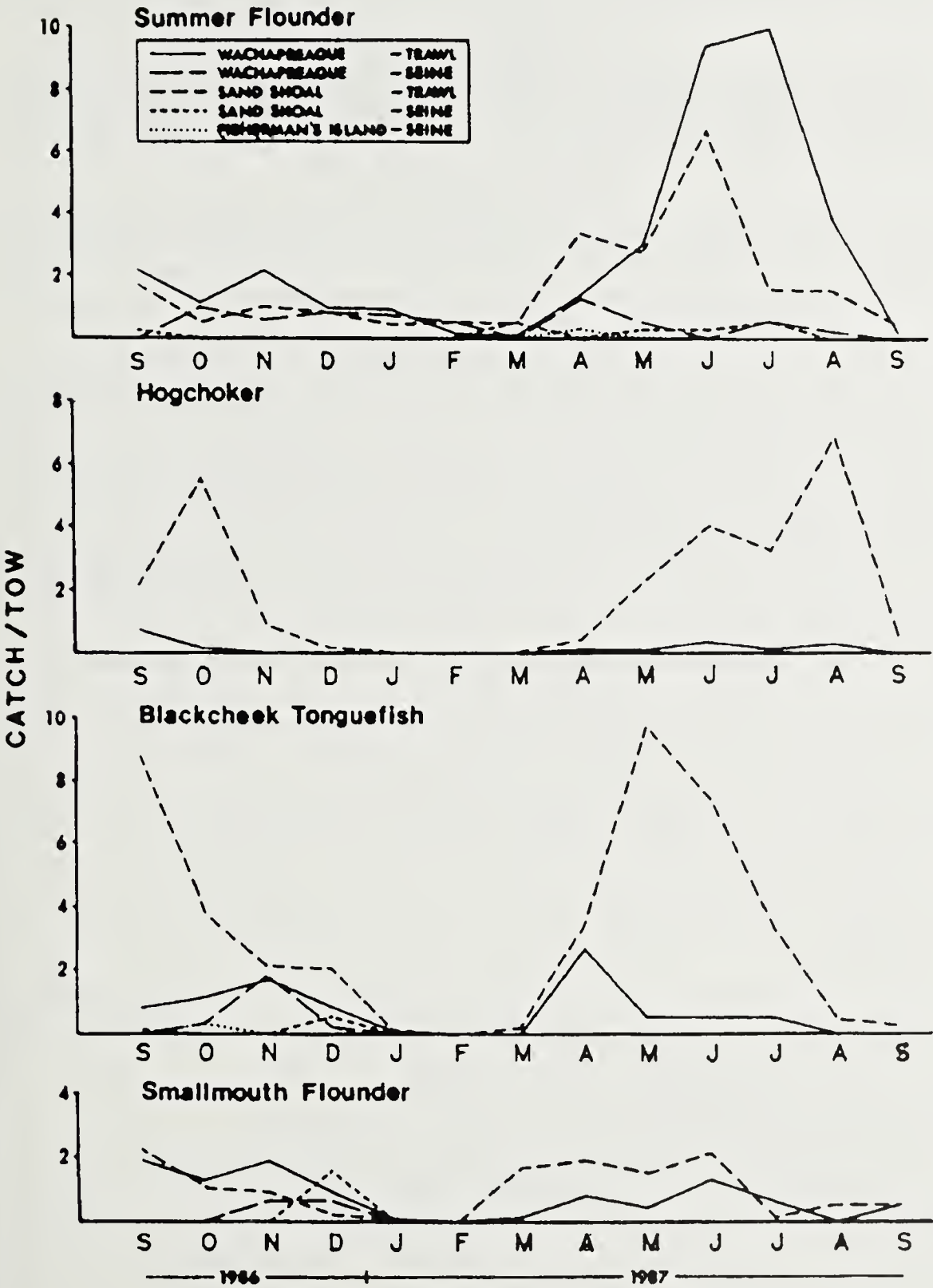


FIGURE 11. Catch/tow (5 min trawl or 25 m seine) of dominant flatfishes by site, September 1986 - September 1987.

different techniques employed, no conclusions can be made regarding relative changes in species composition over time.

ACKNOWLEDGEMENTS

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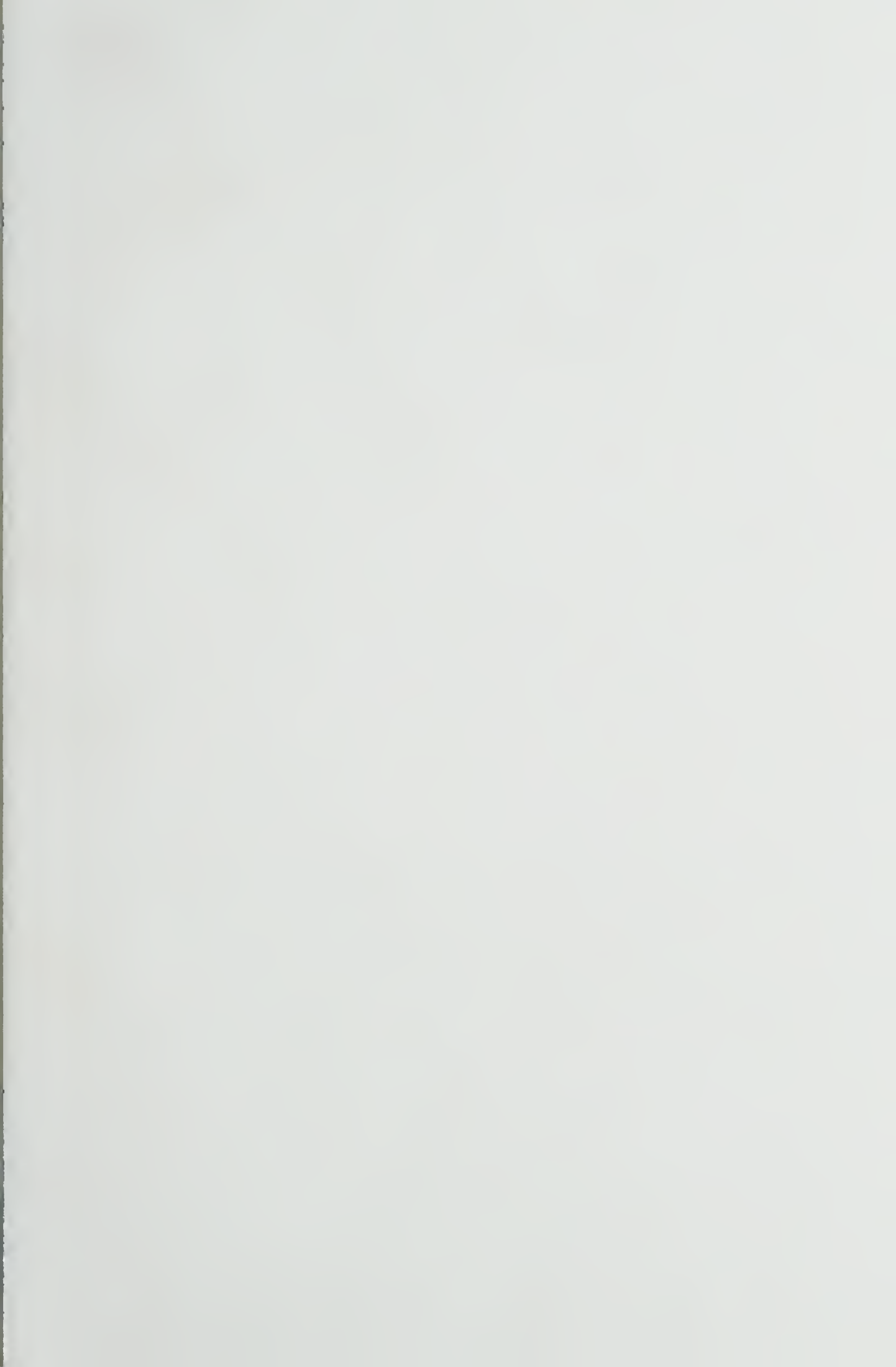
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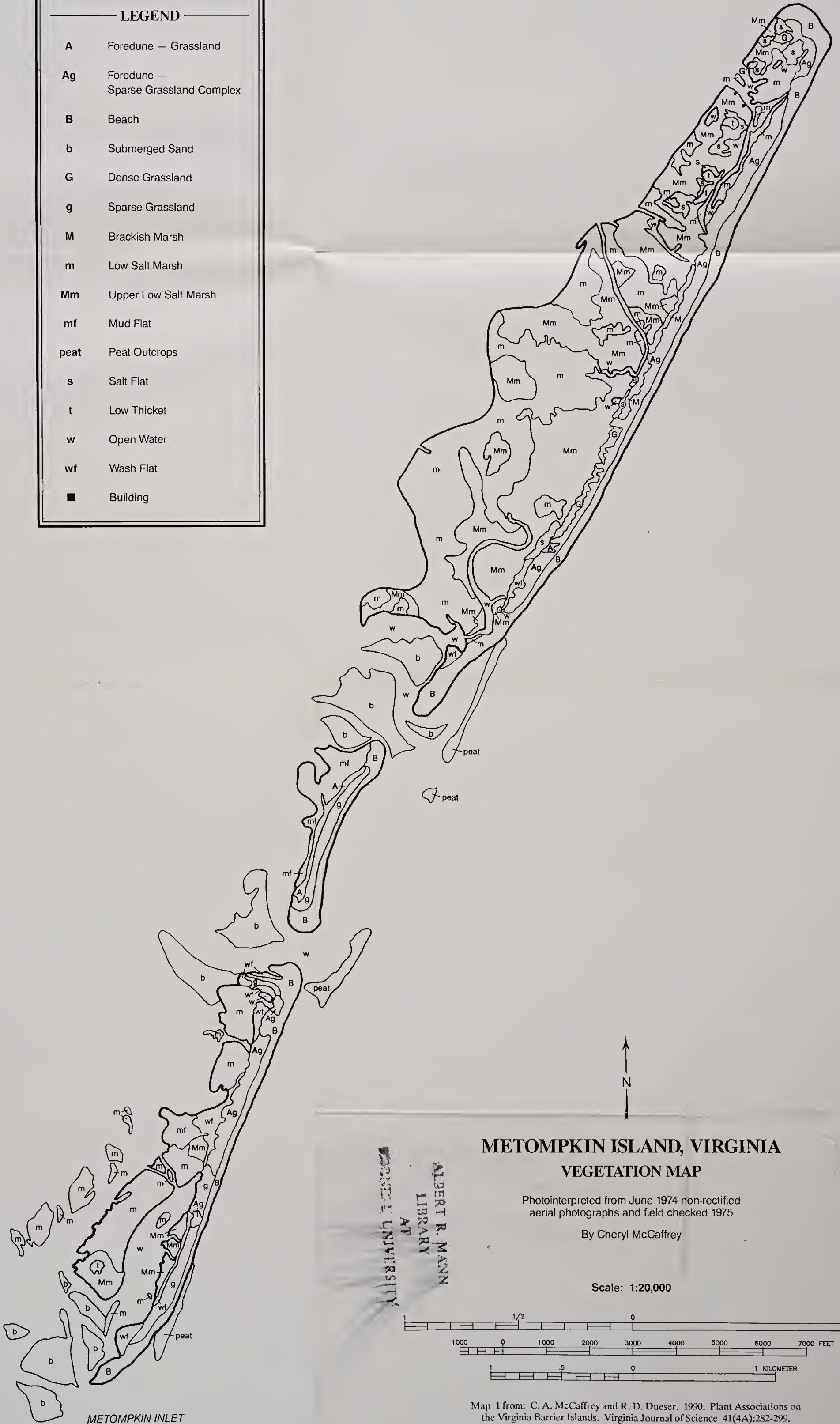
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| LEGEND | |
|--------|--|
| A | Foredune — Grassland |
| Ag | Foredune — Sparse Grassland Complex |
| B | Beach |
| b | Submerged Sand |
| G | Dense Grassland |
| g | Sparse Grassland |
| M | Brackish Marsh |
| m | Low Salt Marsh |
| Mm | Upper Low Salt Marsh |
| mf | Mud Flat |
| peat | Peat Outcrops |
| s | Salt Flat |
| t | Low Thicket |
| w | Open Water |
| wf | Wash Flat |
| ■ | Building |

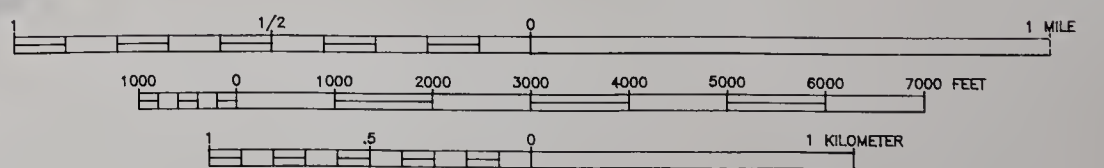


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By Cheryl McCaffrey

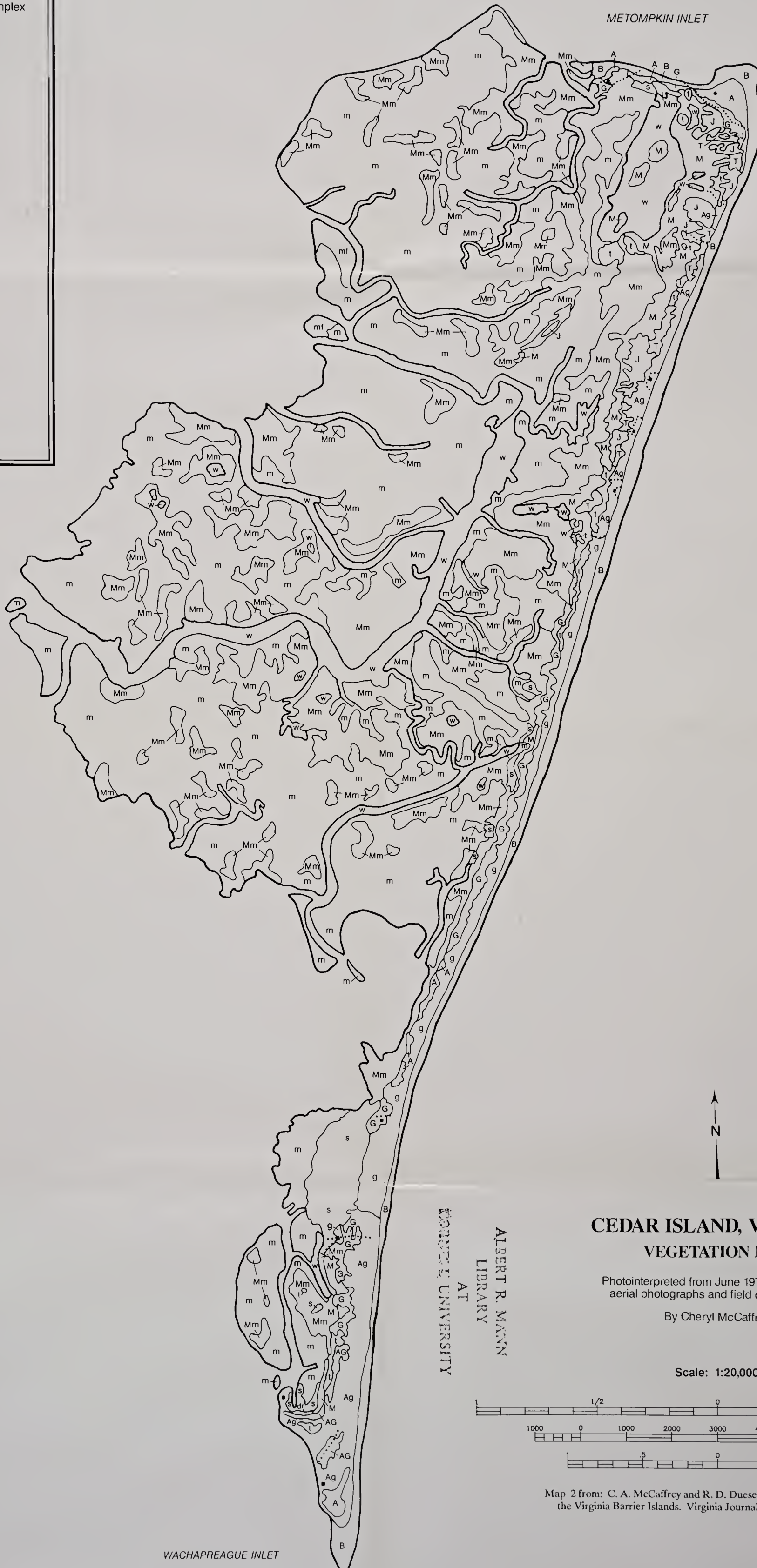
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Map 1 from: C. A. McCaffrey and R. D. Dueser. 1990. Plant Associations on
the Virginia Barrier Islands. Virginia Journal of Science 41(4A):282-299.

LEGEND

- A Foredune — Grassland
- AG Beachgrass Dunes — Dense Grassland Complex
- Ag Foredune — Sparse Grassland Complex
- B Beach
- dr Drift
- G Dense Grassland
- g Sparse Grassland
- J Juniper
- M Brackish Marsh
- m Low Salt Marsh
- Mm Upper Low Salt Marsh
- s Salt Flat
- T Tall Thicket
- t Low Thicket
- w Open Water
- Roadway
- Building

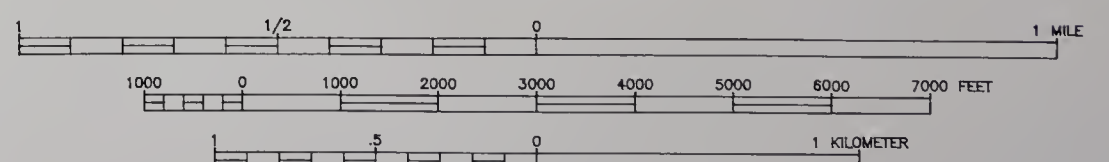


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By Cheryl McCaffrey

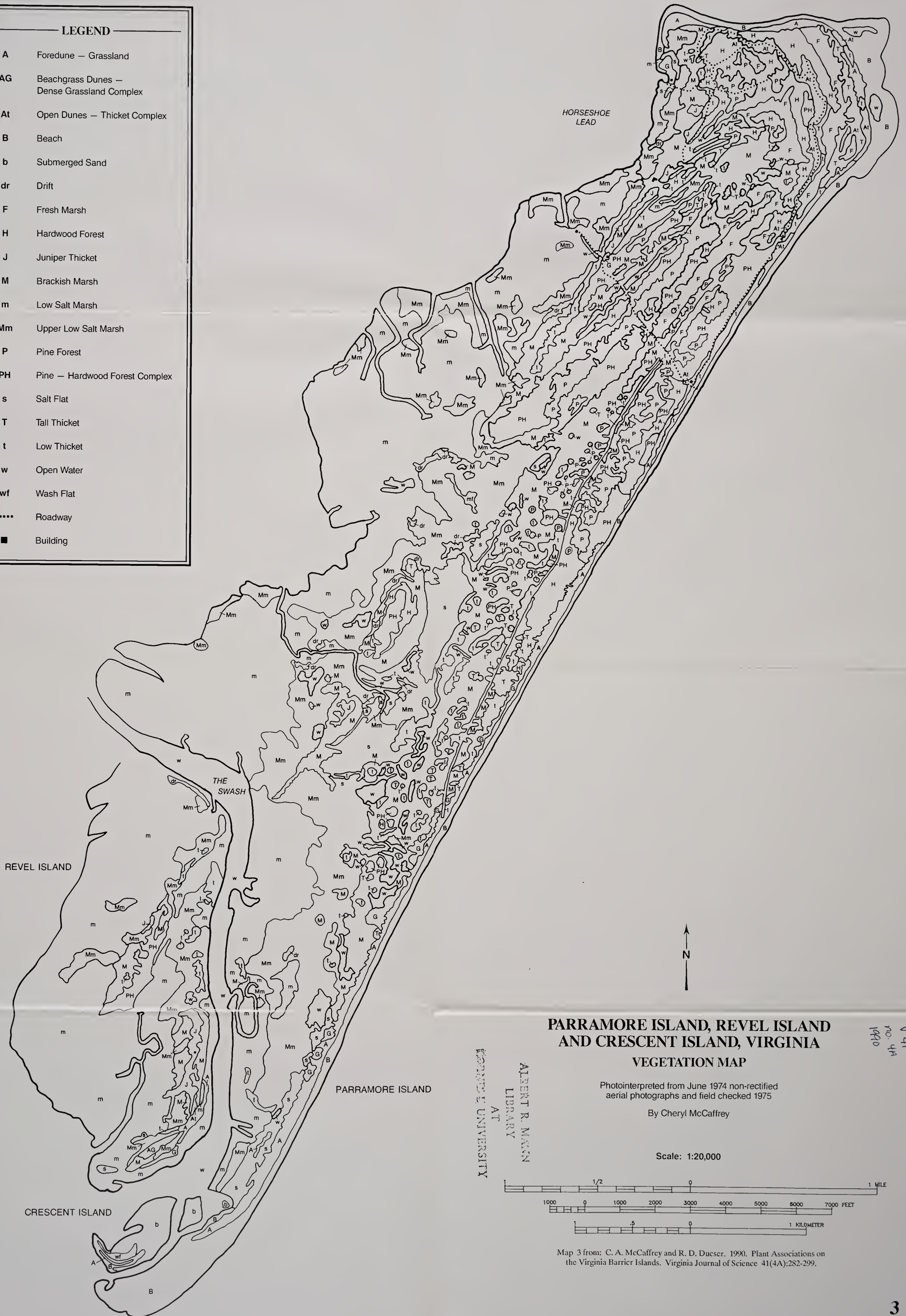
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Map 2 from: C. A. McCaffrey and R. D. Dueser. 1990. Plant Associations on
the Virginia Barrier Islands. Virginia Journal of Science 41(4A):282-299

LEGEND

- A Foredune — Grassland
- AG Beachgrass Dunes — Dense Grassland Complex
- At Open Dunes — Thicket Complex
- B Beach
- b Submerged Sand
- dr Drift
- F Fresh Marsh
- H Hardwood Forest
- J Juniper Thicket
- M Brackish Marsh
- m Low Salt Marsh
- Mm Upper Low Salt Marsh
- P Pine Forest
- PH Pine — Hardwood Forest Complex
- s Salt Flat
- T Tall Thicket
- t Low Thicket
- w Open Water
- wf Wash Flat
- Roadway
- Building

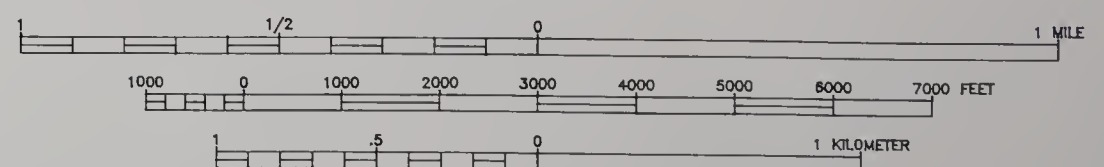


PARRAMORE ISLAND, REVEL ISLAND AND CRESCENT ISLAND, VIRGINIA VEGETATION MAP

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aerial photographs and field checked 1975

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Q
181
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1990

LEGEND

A

Foredune — Grassland

AG

Beachgrass Dunes — Dense Grassland Complex

AT

Open Dunes — Tall Thicket Complex

B

Beach

dr

Drift

F

Fresh Marsh

G

Dense Grassland

g

Sparse Grassland

M

Brackish Marsh

m

Low Salt Marsh

Mm

Upper Low Salt Marsh

s

Salt Flat

T

Tall Thicket

t

Low Thicket

uw

Underwater Flora (or Fauna)

w

Open Water

wf

Wash Flat

.....

Roadway

■

Building



Q
1-
v81
v41
no. 47
1990

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Map 5 from: C. A. McCaffrey and R. D. Dueser. 1990. Plant Associations on the Virginia Barrier Islands. Virginia Journal of Science 41(4A):282-299.

LEGEND

A

Foredune — Grassland

AG

Beachgrass Dunes — Dense Grassland Complex

B

Beach

b

Submerged Sand

G

Dense Grassland

g

Sparse Grassland

M

Brackish Marsh

m

Low Salt Marsh

Mm

Upper Low Salt Marsh

mf

Mud Flat

peat

Peat Outcrops

s

Salt Flat

t

Low Thicket

w

Open Water

wf

Wash Flat

.....

Roadway

■

Building



181
V 41
no. 4A
1990

LEGEND

A

Foredune — Grassland

B

Beach

b

Submerged Sand

dr

Drift

G

Dense Grassland

g

Sparse Grassland

m

Low Salt Marsh

Mm

Upper Low Salt Marsh

s

Salt Flat

T

Tall Thicket

uw

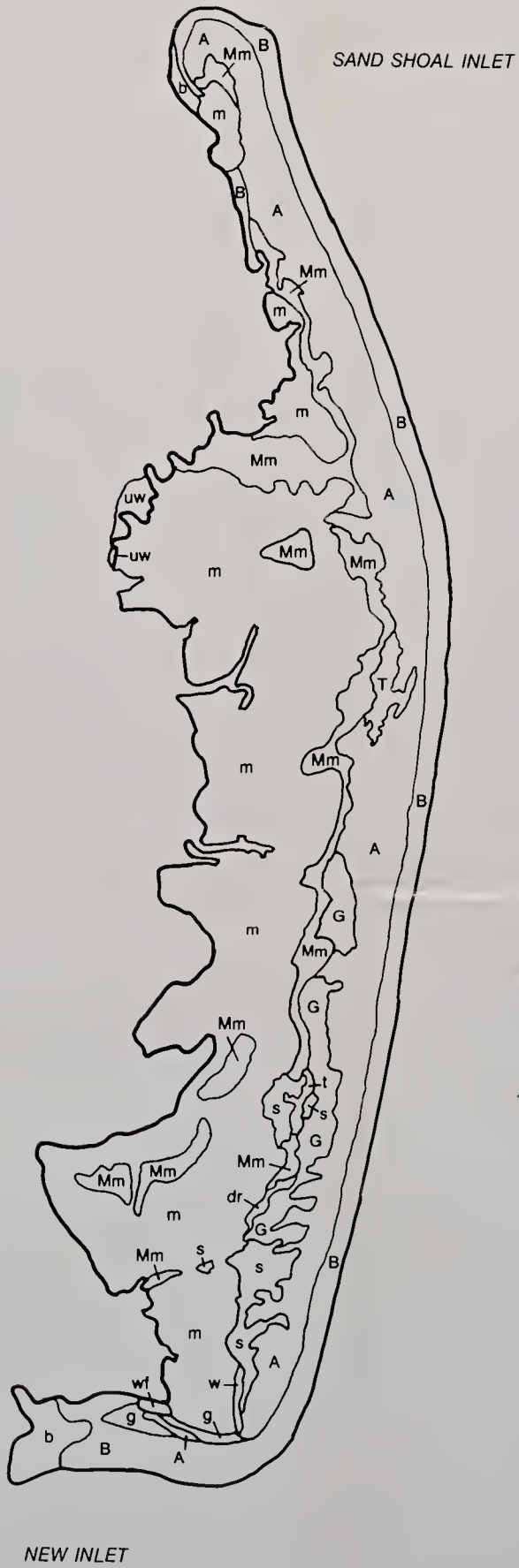
Underwater Flora (or Flauna)

w

Open Water

wf

Wash Flat

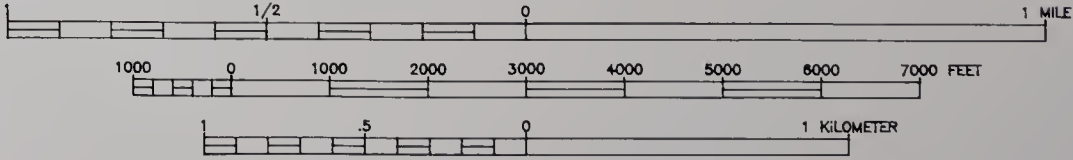


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WRECK ISLAND, VIRGINIA
VEGETATION MAP

Photointerpreted from June 1974 non-rectified
aerial photographs and field checked 1975
By Cheryl McCaffrey

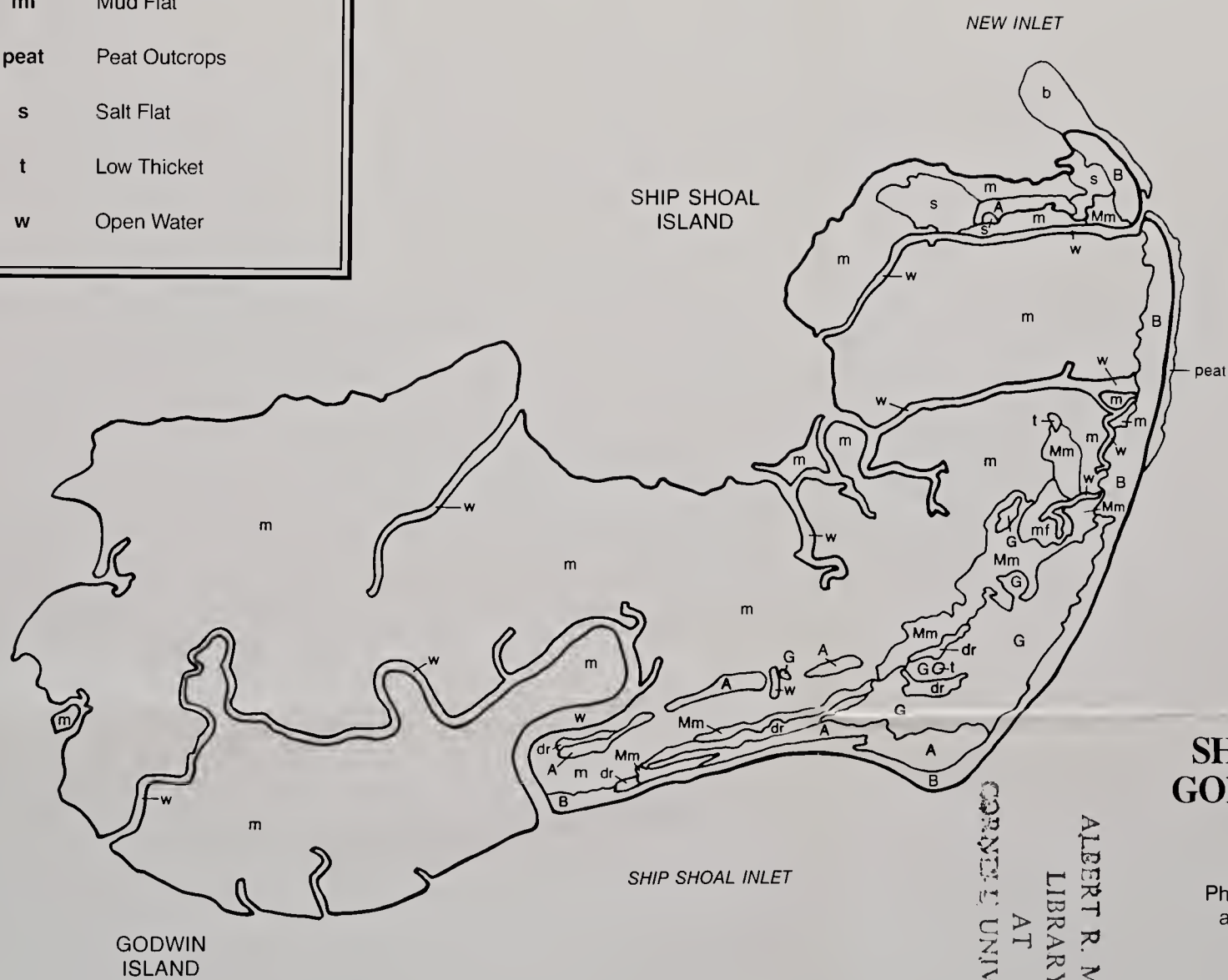
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Map 7 from: C. A. McCaffrey and R. D. Dueser. 1990. Plant Associations on
the Virginia Barrier Islands. Virginia Journal of Science 41(4A):282-299.

Q
1
V81
V. 41
no. 4A
1990

| LEGEND | |
|--------|----------------------|
| A | Foredune — Grassland |
| B | Beach |
| b | Submerged Sand |
| dr | Drift |
| G | Dense Grassland |
| m | Low Salt Marsh |
| Mm | Upper Low Salt Marsh |
| mf | Mud Flat |
| peat | Peat Outcrops |
| s | Salt Flat |
| t | Low Thicket |
| w | Open Water |

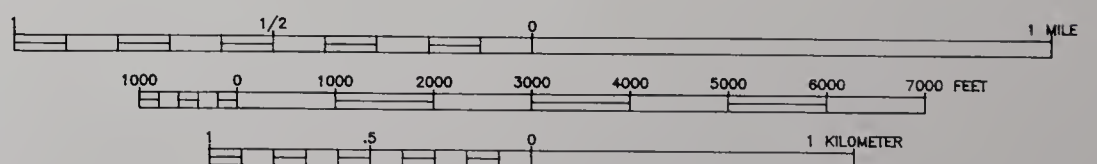


SHIP SHOAL ISLAND AND GODWIN ISLAND, VIRGINIA VEGETATION MAP

Photointerpreted from June 1974 non-rectified
aerial photographs and field checked 1975

By Cheryl McCaffrey

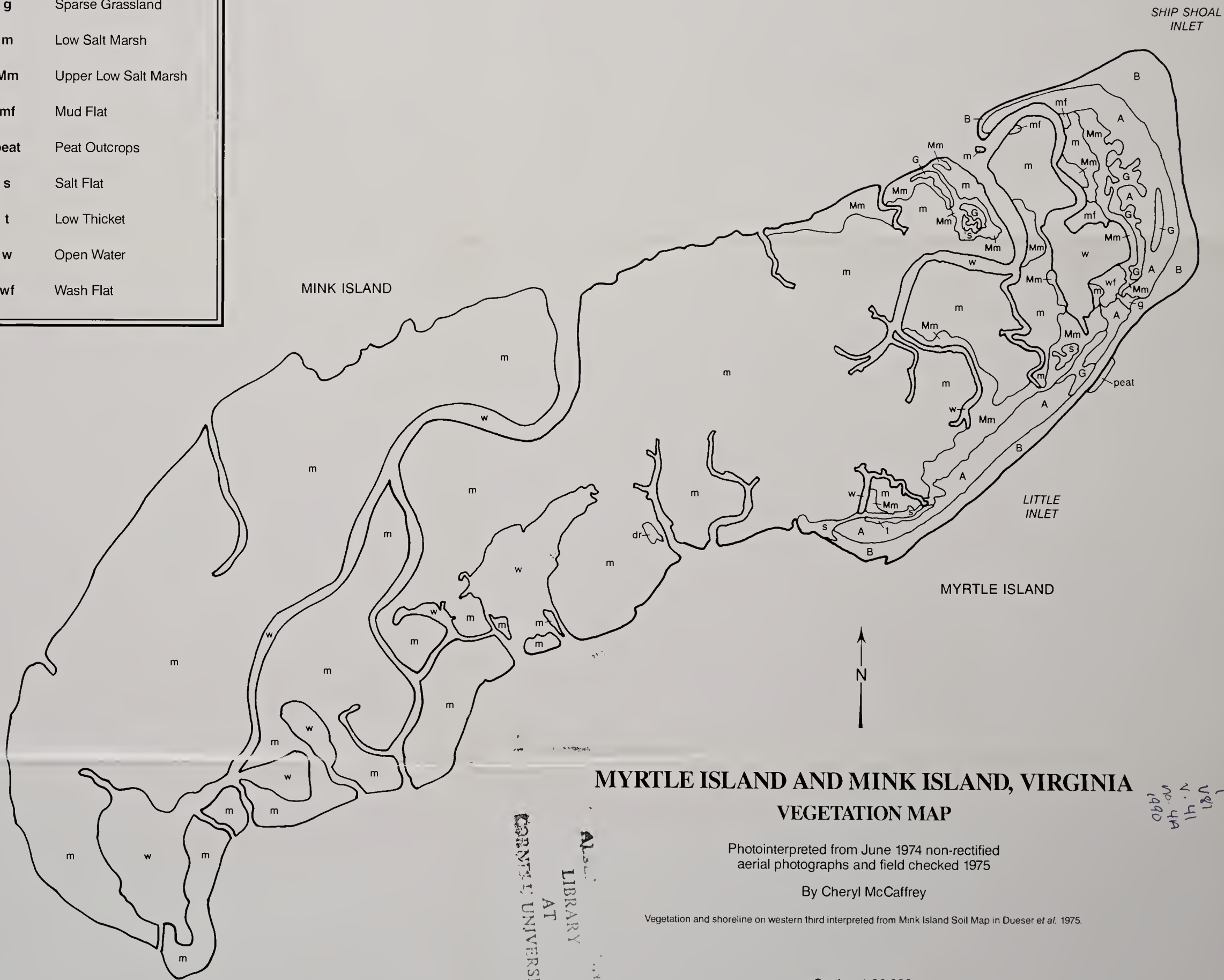
Scale: 1:20,000



Map 8 from: C. A. McCaffrey and R. D. Dueser. 1990. Plant Associations on
the Virginia Barrier Islands. Virginia Journal of Science 41(4A):282-299.

Q
V81
V-41
NO. 47
1990

| LEGEND | |
|--------|----------------------|
| A | Foredune — Grassland |
| B | Beach |
| dr | Drift |
| G | Dense Grassland |
| g | Sparse Grassland |
| m | Low Salt Marsh |
| Mm | Upper Low Salt Marsh |
| mf | Mud Flat |
| peat | Peat Outcrops |
| s | Salt Flat |
| t | Low Thicket |
| w | Open Water |
| wf | Wash Flat |



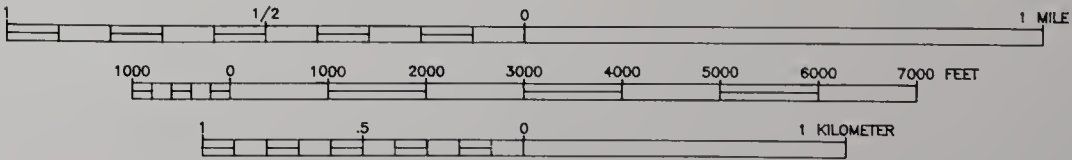
MYRTLE ISLAND AND MINK ISLAND, VIRGINIA VEGETATION MAP

Photointerpreted from June 1974 non-rectified
aerial photographs and field checked 1975

By Cheryl McCaffrey

Vegetation and shoreline on western third interpreted from Mink Island Soil Map in Dueser *et al.* 1975.

Scale: 1:20,000



Map 9 from: C. A. McCaffrey and R. D. Dueser. 1990. Plant Associations on
the Virginia Barrier Islands. *Virginia Journal of Science* 41(4A):282-299.

| LEGEND | |
|--------|-------------------------------------|
| A | Foredune — Grassland |
| Ag | Foredune — Sparse Grassland Complex |
| B | Beach |
| dr | Drift |
| F | Fresh Marsh |
| G | Dense Grassland |
| g | Sparse Grassland |
| H | Hardwood Forest |
| M | Brackish Marsh |
| m | Low Salt Marsh |
| Mm | Upper Low Salt Marsh |
| mf | Mud Flat |
| PH | Pine — Hardwood Complex |
| peat | Peat Outcrops |
| s | Salt Flat |
| T | Tall Thicket |
| t | Low Thicket |
| uw | Underwater Flora (or Fauna) |
| w | Water |
| wf | Wash Flats |
| | Roadway |
| ■ | Building |

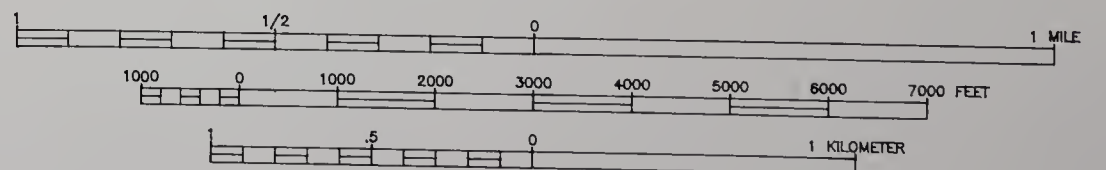


SMITH ISLAND, VIRGINIA VEGETATION MAP

Photointerpreted from June 1974 non-rectified
aerial photographs and field checked 1975

By Cheryl McCaffrey

Scale: 1:20,000



Map 10 from: C. A. McCaffrey and R. D. Dueser. 1990. Plant Associations on
the Virginia Barrier Islands. Virginia Journal of Science 41(4A):282-299.

V 81
V. 41
no 44
1980

